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CHROMOSOME NUMBERS AND DIMENSIONS, SPECIES-FORMATION AND PHYLOGENY IN THE GENUS CAREX

BY *O. HEILBORN*
STOCKHOLM

I. INTRODUCTION.

IN 1900 JUEL published his study on *Carex acuta* L. (*C. gracilis* CURT.), this being the first investigation made on the cytology of the genus *Carex*. JUEL'S work deals principally with the pollen-development of the above-mentioned species and, with respect to this process, the studies of the present writer have merely confirmed his observations, nothing of importance having been found to be added. As to the number of the chromosomes, however, JUEL'S work does not give any exact data (cf. below).

The next work on the cytology of *Carex* was that of STOUT (1913), dealing with the chromosomes of *C. aquatilis* WG. This author confirms and completes the work of JUEL on the pollen-development and, furthermore, he makes a very thorough study of the whole chromosome cycle, special emphasis being laid on the individuality of the chromosomes and their serial arrangement. As to these two problems, STOUT states that the chromosomes of *C. aquatilis* can be seen as small spherical bodies, maintaining their individuality and a serial arrangement in all cells and in all stages of development except in synizesis.

To these latter statements the present writer wants, however, to make some remarks. In really resting nuclei, such as are found *e. g.* in the walls of the carpels or in the bracts of the inflorescences, I have not been able to see any chromosomes and hence I suppose that the »resting» stages, studied by STOUT, were in reality *interphases* (cf. LUNDEGÅRDH 1913). This is especially likely to be the case as the somatic cells investigated belonged principally to the rapidly dividing tissues of root-tips, where the resting stage as a rule is but seldom attained.

The present writer began his studies on *Carex* in 1916 and a first preliminary account was published in 1918 (HEILBORN 1918). In this work some remarks are made on the shape of the chromosomes in *Carex* and on their serial arrangement according to STOUT. It is stated (p. 216) that »diese Chromosomenketten habe ich auch und zwar in einigen Prophasen ziemlich deutlich gesehen; jedoch ist es wohl fraglich, ob die Chromosomen nur in einer, einfachen, zusammenhängenden Kette liegen». Later I observed that the chromosomes in the prophases of the pollen-cell nuclei (*i. e.* after the reduction division) as a rule are rather regularly arranged, reappearing in the same position as they occupied in the preceding homotypic division and thus lying more or less parallel and directed against the pole of the fore-going division (cf. chapt. 3). This regularity may give, if the chromosomes are short and more or less spherical, a certain impression of serial arrangement. If the nuclei, however, contain very long chromosomes, as is the case in some species (cf. chapt. 3), no »serial» arrangement can be found. Hence the present writer is inclined to regard the »serial» arrangement, described by STOUT and sometimes found by himself, too, as a result of the above described regularity in arrangement, quite analogous with that found by BOVERI (1887 ff., 1909) in *Ascaris*. It seems very likely that this explanation will hold good for the somatic nuclei, too, of which STOUT has described and figured a considerable number. It is, nevertheless, possible that there really exist some kind of chromosome series in the nuclei of *Carex,* expressing themselves *e. g.* in a more or less regular arrangement of the chromosomes in the metaphase plates of the heterotypic division of the P. M. C., seen in polar view. This should probably be regarded as an expression of affinity between homologous gemini which arrange themselves in short rows of, generally, 3—5 (fig. 1—2, Pl. I). It is likely that homologous gemini really exist in the nuclei of most of the *Carex*-species, their existence being due to chromosome duplication (cf. chapt. 6). It seems, however, quite excluded that all the chromosomes should be arranged in one single, continuous thread.

As to the shape of the chromosomes, I stated already in the above-mentioned work (p. 219) that the chromosomes in the pollen-cell prophases of *C. ericetorum* have »die Form von kurzen Stäbchen, und in früheren Stadien — — dünnen, gebogenen Fäden». The same has been found to be the case with several other species (chapt. 3) with low chromosome numbers. Though it is somewhat difficult to

determine the chromosome shape in species with high numbers, it seems, however, extremely likely that the above facts hold good also for such species, as the different *size-classes* reappear in several of them (cf. chapt. 3). Thus long and short chromosomes are found in *C. glauca* as well as in *C. panicea* and others. STOUT's statement that the chromosomes in *C. aquatilis* have the shape of small, spherical bodies in all stages (except synizesis) seems, therefore, very unlikely and is probably due to some misinterpretation of the microscopical slides.

Summarizing we may state, with regard to STOUT's work, that the chromosomes in *Carex* can not be seen as individual bodies in all stages of development, that the »serial» arrangement is a rather doubtful phenomenon, the existence of which has not been proved with any degree of certainty, and that the chromosomes do not appear as spherical bodies throughout the whole developmental cycle.

The foregoing critical remarks on STOUT's work have been made already here in the introduction, as they fall somewhat beside the principal topic of the present work, *viz.* the chromosome numbers and their bearing on the problems of species-formation and phylogeny in the genus *Carex*. The first chromosome number within this genus was reported by JUEL who counted ca. 52 chromosomes in a slide of *C. acuta,* not laying much stress, however, on the exact determination of the number. Some of his paraffin material he gave to prof. ROSENBERG and a slide, cut of this material, was later handed over to me. In this slide I found several very good metaphase plates of the heterotypic division in the P. M. C., each showing clearly 42 chromosomes, which thus is the haploid number in this species. Looking at the plate, figured by JUEL, one can not avoid the impression that it might be a beginning anaphasis rather than a metaphasis and that the dumbbell-shape of the chromosomes, often found in these stages and expecially conspicuous in the beginning anaphasis, may have been responsible for the high number reported, some dumbbell-shaped chromosomes probably having been counted as two each. STOUT counted ca. 37 chromosomes (haploid) in several stages of *C. aquatilis* and, judging from his good drawings, we feel sure that it must be a rather safe figure.

The present writer in his first paper (1918) gave some chromosome numbers which were, however, erroneous, the right figures being given in a second paper (HEILBORN 1922) in addition to a lot of new numbers. The right number of *C. gracilis* was also published

in the latter paper. Here, further, it was stated that no multiple chromosome numbers exist in this genus, the numbers being quite irregular and ranging from 9 to 42. From a study on the dimensions of the chromosomes, the details of which were not published then but are found in chapt. 3 in the present paper, the conclusion was drawn that the genus *Carex* does not contain any polyploid species. It thus appeared that *Carex* — with regard to the chromosome numbers — occupies a rather unique position within the vegetable kingdom and that a closer cytological investigation of this genus would, probably, reveal interesting facts concerning the problems of species-formation and phylogeny in the genus.

The lines along which this investigation has been carried out are the following: determination of chromosome numbers, analysis of chromosome dimensions, searching for irregularities in meiosis by which new numbers might arise and investigation of the distribution of the chromosome numbers on the different systematic groups of the genus (chapt. 2—5). By combination of all the facts, thus brought together, the writer has been able to form certain opinions as to the origin of the chromosome numbers, the process of species-formation and the phylogeny of the genus (chapt. 6—8). In chapt. 8 an attempt is also made to combine chromosome numbers with geographical distribution and in chapt. 9 comparisons are made with some other cytologically investigated plant genera.

The material investigated has been collected either in nature or in the Bergianic Garden (Hortus Bergianus) at Stockholm. Most of the material, collected in nature by the present writer, has been gathered at Djursholm in the neighbourhood of Stockholm, some outside Visby on the island Gotland and some, finally, at Bodö and Tromsö in northern Norway. The material has been fixed in FLEMMING'S solution. Before fixing the spikes have been cut in pieces, immersed for a few moments in alcohol and slightly squeezed, the air behind the bracts thus being removed. After a slight washing in water they have then been put in the fixing fluid. All slides have been stained in HEIDENHAIN'S iron haematoxylon. — The technical difficulties of collecting and preparing material of *Carex* are considerable. It is necessary to fix early in spring (in Sweden) when the spikes just appear within the leaf-rosettes, and the species are difficult to find and identify. Hence the best way of working is to collect the plants one year, either marking them in nature or planting them in a garden, and to fix them next spring. Further it is difficult to

fix at the right moment, when the reduction division is carried out, all flowers and spikes of a species passing the same stages more or less simultaneously. Finally the fixing fluid acts very irregularly, some nuclei being excellently fixed but most of them being totally useless. These difficulties are responsible for the incompleteness of the present work.

It is my pleasant duty to thank all persons that have in one way or other facilitated my work, in the first place the professors G. LAGERHEIM and O. ROSENBERG who have been my teachers and have always taken much interest in the progress of this investigation. Further I am indebted to professor O. JUEL for material of *C. gracilis*, to prof. R. E. FRIES, director of the Hortus Bergianus, for permitting me to use the collection of *Carex*-species in this garden, to dr M. G. STÅLFELT, lecturer in this university, dr ELISABETH SCHIEMANN of Berlin and fil. mag. H. VALLIN of Lund for providing further material, to dr G. TÄCKHOLM, lecturer in this university, for material and many good suggestions, fil. kand. E. SÖDERBERG, assistant at Hortus Bergianus, for much valuable help, and mr A. NOTØ, headmaster at Bodö, for several informations. I am also very much indebted to prof. T. G. HALLE of the palaeobotanical department at the State's Museum of Stockholm for permitting me to use the photographical equipment of his department, and to fil. lic. R. FLORIN, assistant at the palaeobotanical department, for much valuable help in taking the photomicrographs of Pl. I. Finally I wish to thank dr G. SAMUELSSON, lecturer in the university of Uppsala, for kindly revising the names of some of the forms investigated.

II. CHROMOSOME NUMBERS.

The chromosome numbers of the different species have, as a rule, been counted in the metaphase plates of the heterotypic division in the P. M. C. (pollen mother-cells), some additional countings, too, having been made in diakineses and in metaphases of the homotypic division in the P. M. C. or in prophases and metaphases of the pollen-cell nuclei. Somatic nuclei, again, cannot be used for counting purposes. Generally the plates counted have been very satisfactorily fixed and the numbers, therefore, exactly determined (cf. the photomicrographs). Those that have not been determined with perfect accuracy are marked with a *ca.* in the following table.

TABLE 1. *Haploid chromosome numbers in Carex, arranged according to the system of* KÜKENTHAL *(1909).*

Subgenus *Primocarex* KÜKENTH.
Sect. *Dioicae* TUCKERM.
C. dioica L. (Hort. Berg. from Finse, Norway) 26
Sect. *Petraeae* O. F. LANG.
C. rupestris ALL. (from Tromsö) 25

Subgenus *Vignea* (P. BEAUV.) NEES.
Sect. *Arenariae* KUNTH.
C. intermedia GOOD. (= *disticha* HUDS., fr. Djursholm) ca. 31
Sect. *Muehlenbergianae* TUCKERM.
C. contigua HOPPE (fr. Djursholm) ..... ca. 29
C. divulsa GOOD. **Leersii* (F. SCHULTZ) W. KOCH (Hort. Berg. fr. Stenshuvud, Scania, Sweden) 29
Sect. *Stenorhynchae* TH. HOLM.
C. vulpina L. (fr. Djursholm) 34
Sect. *Paniculatae* KUNTH.
C. paradoxa WILLD. (fr. Bodö) 32
Sect. *Canescentes* FRIES.
C. canescens L. (fr. Tromsö) 28
Sect. *Tenuiflorae* KUNTH.
C. loliacea L. (Hort. Berg. fr. Paddos (?)) 27
Sect. *Elongatae* KUNTH.
C. elongata L. (fr. Djursholm) ..... ca. 28

Subgenus *Eucarex* COSS. et GERM.
Sect. *Acutae* FRIES.
Subsect. *Rigidae* FRIES.
C. rigida GOOD. (Hort. Berg. fr. Fjällnäs, Sweden) 35
Subsect. *Vulgares* ASCHERS.
C. aquatilis WAHLENB. (cf. STOUT 1913) ..... ca. 37
C. Goodenoughii GAY (fr. Djursholm) 42
var. *juncea* FRIES (Hort. Berg.) ..... ca. 42
C. gracilis CURT. (Uppsala Bot. Gard. and Hort. Berg. spont.) 42
Subsect. *Caespitosae* FRIES.
C. caespitosa L. (fr. Djursholm) 40
C. Hudsonii A. BENN. (× *Goodenoughii* GAY? — fr. Djursholm) 40
Sect. *Atratae* KUNTH.
C. alpina SWARTZ. (Hort. Berg. fr. Norway) 28

C. Buxbaumii WAHLENB. (Hort. Berg. fr. Jämtland, Sweden) ..... ca. 37
C. atrata L. (Hort. Berg.) 27
Sect. *Trachychlaenae* DREJER.
C. glauca MURR. (et SCOP.) (fr. Visby) 38
Sect. *Pachystylae* KÜKENTH.
C. pallescens L. (fr. Djursholm) 32
C. tomentosa L. (fr. Visby) 24
Sect. *Montanae* FRIES.
C. ericetorum POLL. (fr. Djursholm) 15
C. montana L. (Hort. Berg.) 19
C. pilulifera L. (fr. Djursholm) 9
Sect. *Mitratae* KÜKENTH.
C. caryophyllea LATOURR. (fr. Djursholm) 31
Sect. *Digitatae* FRIES.
C. digitata L. (fr. Djursholm) 26
C. ornithopoda WILLD. (fr. Visby) ..... ca. 23
Sect. *Paniceae* TUCKERM.
C. panicea L. (fr. Djursholm) 16
C. sparsiflora (WAHLENB.) STEUD. (= *vaginata* TAUSCH., Hort. Berg. fr. Fjällnäs, Sweden and Valdres, Norway) 16
Sect. *Hymenochlaenae* DREJER.
C. capillaris L. (Hort. Berg. fr. Skellefteå, Sweden) 27
Sect. *Spirostachyae* DREJER.
C. punctata GAUD. (Hort. Berg.) 34
C. distans L. (fr. Visby) 37
C. Hornschuchiana HOPPE (fr. Visby) 28
C. flava L. × *Hornschuchiana* HOPPE (probably; fr. Bodö) 33
C. Oederi (EHRH.) HOFFM. (fr. Djursholm) 35
C. lepidocarpa TAUSCH. (Hort. Berg. fr. Kävlinge, Scania, Sweden and fr. Visby) 34
Sect. *Pseudo-cypereae* TUCKERM.
C. pseudo-cyperus L. (fr. Djursholm) 33
Sect. *Physocarpae* DREJER.
Subsect. *Lupulinae* TUCKERM.
C. Grayi CAREY (Hort. Berg. fr. Zürich Bot. Garden) .. 26
Subsect. *Vesicariae* TUCKERM.
C. rostrata STOKES (fr. Djursholm) 38
C. vesicaria L. (fr. Djursholm) 41

Sect. *Paludosae* FRIES.
C. riparia CURT. (fr. Djursholm) 36
Sect. *Hirtae* TUCKERM.
C. hirta L. (Hort. Berg.) 56

To the above table some taxonomical remarks must be made. As mentioned in the introduction, G. SAMUELSSON has kindly revised the names of several of the species and forms here investigated. According to him, the specimens that had previously been referred to *C. flava* by the present writer (HEILBORN 1922), belong to *C. Oederi,* while the specimen, previously referred to *C. Hudsonii,* should be *C. Goodenoughii* × *Hudsonii.* Further the *divulsa*-form investigated should most probably be *C. divulsa* **Leersii* (F. SCHULTZ) W. KOCH and the *Hornschuchiana*-like form from Bodö should probably be that species or a hybrid between it and some other one. Regarding the presumed hybrid *C. Goodenoughii* × *Hudsonii,* it must be remarked that the former of these species has 42 chromosomes (haploid). Hence an F_1-individual of the hybrid must necessarily show at least this chromosome number (of which probably some univalents). In F_2 an elimination of some chromosomes might take place, though, according to the opinions developed in chapt. 6, this does not seem very probable in the present case. It seems likely that hybrids of *Carex* behave like *Lepidoptera* as regards the meiotic divisions (FEDERLEY 1913), *i. e.* it seems likely that univalent chromosomes divide in meiosis and are kept in the following generations, whereas a decrease in chromosome number during subsequent hybrid generations probably does not occur. In other words, the number $X = 40$ in the form under consideration makes it impossible that this form should belong to the F_1-generation of the above hybrid, while it possibly, but not very probably, might belong to a later generation. The present writer is still inclined to believe that this form might be a modification of *C. Hudsonii.* As to the *Hornschuchiana*-like form, it cannot be the pure species, because it has 33 chromosomes, while typical *Hornschuchiana* has only 28. According to BLYTT and DAHL (1906), *C. Hornschuchiana* does not reach Bodö (67 $^1/_3$°) but stops at Alstenö (66°), while the subspecies *fulva* GOOD., generally regarded as a hybrid between *C. flava* and *C. Hornschuchiana,* has its northern limit at Bodö. Probably the form, here dealt with, belongs to the last-mentioned hybrid. It is then interesting to note that this apparently hybrid race occurs outside the limits of one of the parents and, further,

that it has a quite normal reduction division and a chromosome number much higher than that of *C. Hornschuchiana* and probably very near the number of *C. flava.* The latter facts agree very well with the assumption that the meiotic divisions in *Carex*-hybrids are carried out according to the *Pygaera*-scheme of FEDERLEY (cf. chapt. 6). It should, in addition, be pointed out that this *Hornschuchiana*-hybrid occurs abundantly at Bodö and that, at the place, where the fixation was made, no other representatives of the *Spirostachyae* could be found.

It appears from the above table that the (twenty-two) chromosome numbers, determined with perfect accuracy, are the following ones:

9, 15, 16, 19, 24, 25, 26, 27, 28, 29, 31, 32, 33, 34, 35, 36, 37, 38, 40, 41, 42 and 56.

These numbers cannot be arranged in a series of multiples similar to those, now known from so many other plant genera. In fact, multiple chromosome numbers appear to be a characteristic of most plant genera (higher plants at least) and, consequently, the genus *Carex* seems to constitute an interesting exception from the rule. It is true that irregular numbers are found in other genera, too, but there they occur together with multiples and are, apparently, often of secondary origin. Before proceeding to a full discussion of this problem in chapt. 6 and 9 the dimensions of the chromosomes in *Carex* must, however, be considered in detail.

III. CHROMOSOME DIMENSIONS.

The drawings, accompanying this chapter, as well as the photos on Pl. I, show clearly that, in general, the chromosomes decrease in size when their number increases. The metaphase plates of the different species may be arranged in a rather continuous series (fig. 1, 2), beginning with low numbers and big chromosomes and ending with high numbers and small chromosomes. Apparently some exceptions may be found (*e. g.* fig. 2 b). They might depend on some specific metabolic circumstances, influencing the production of chromatin, if they are not, simply, fixing artefacts. This gradual decrease in chromosome size should be regarded as an expression of a limitation in the cells' capacity of producing chromatin. When the chromosome number increases, the total chromatin amount of the cell probably also increases until an upper limit is reached; later on the chromatin amount does not increase any more but the mean chromosome size decreases. It is clear, under such circumstances, that there cannot be

found any simple relation between chromosome number and size of the nuclei and cells. The present writer is rather inclined to regard the small differences in cell size that are found as dependant on specific genes which may influence not only the size of the cells and nuclei, but also the chromatin production within the nuclei. The

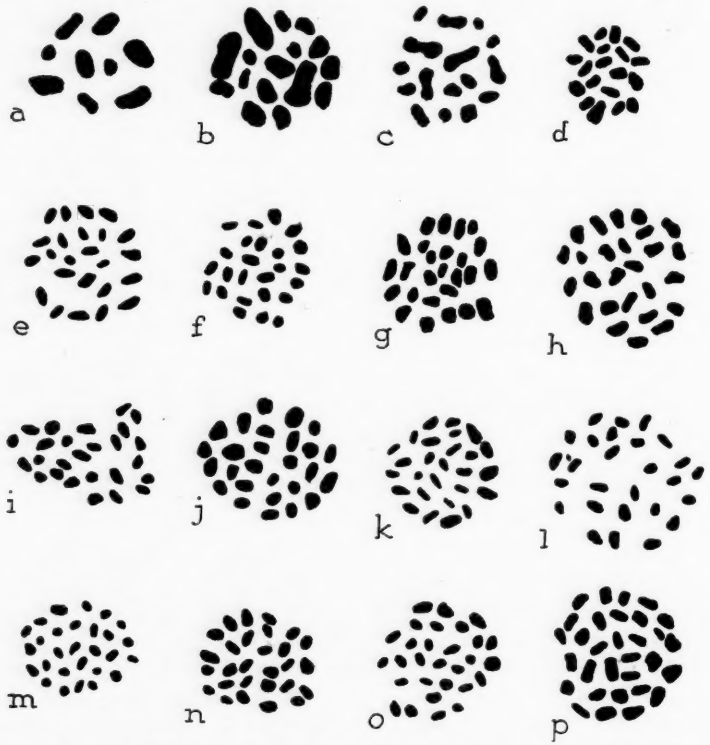

Fig. 1. Heterotypic metaphases in P. M. C. a *C. pilulifera*, b *C. panicea*, c *C. sparsiflora*, d *C. montana*, e *C. tomentosa*, f *C. rupestris*, g *C. dioica*, h *C. digitata*, i *C. Grayi*, j *C. loliacea*, k *C. atrata*, l *C. capillaris*, m *C. alpina*, n *C. Hornschuchiana*, o *C. divulsa* **Leersii*, p *C. caryophyllea*. — REICHERT hom. imm. $^1/_{12}$, LEITZ peripl. oc. 20 × (× 2900).

whole question falls, however, somewhat beside our principal subject and shall, therefore, not be further discussed.

Much more important in this connection are the differences in size and shape that are often found between the chromosomes *within the same nucleus*. Already at an early stage of this investigation

the attention of the present writer was attracted by the conspicuous difference between the three big and the thirteen smaller chromosomes in *C. panicea* and later the chromosome dimensions of several species have been made the object of a rather thorough study.

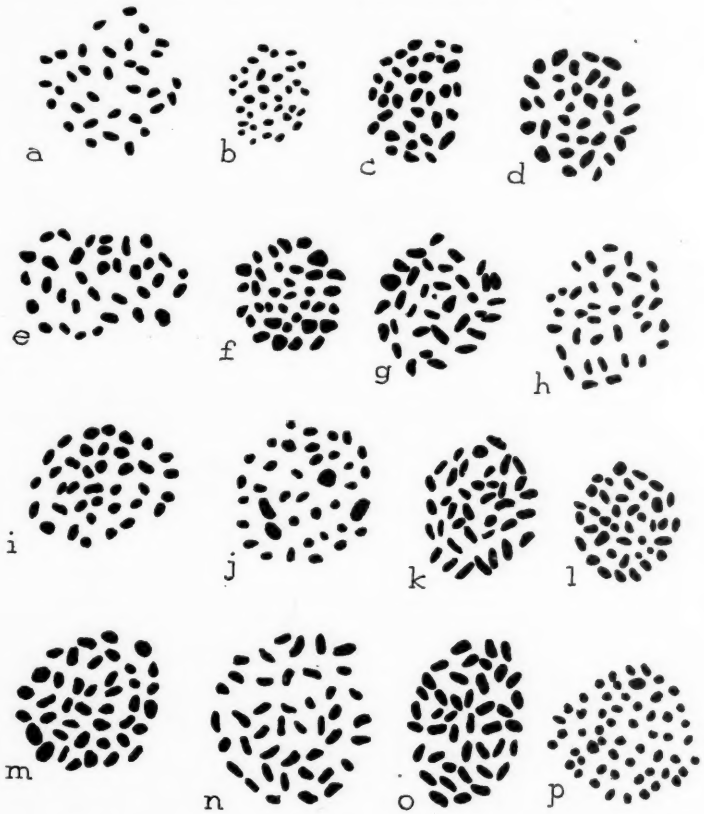

Fig. 2. Heterotypic metaphases in P. M. C. a *C. flava* × *Hornschuchiana* (?), b *C. pseudo-cyperus*, c *C. vulpina*, d *C. punctata*, e *C. lepidocarpa*, f *C. Oederi*, g *C. rigida*, h *C. riparia*, i *C. distans*, j *C. glauca*, k *C. rostrata*, l *C. Hudsonii* (× *Goodenoughii?*), m *C. vesicaria*, n *C. Goodenoughii*, o *C. gracilis*, p *C. hirta*. — REICHERT hom. imm. 1/12, LEITZ periplan. oc. 20 × (× 2900).

These size differences can be traced through several stages of the pollen-development, a fact of some importance, as it shows the differences to depend on real and characteristic properties of the chromo-

somes and not on the physiological conditions of a certain stage of development. Thus the three big chromosomes of *C. panicea* are found in the diakineses and heterotypic metaphases as well as in the prophases and metaphases of the pollen-cell nuclei. In the two last-mentioned stages they set off especially clear from the smaller chromosomes. In the heterotypic metaphases the differences are often somewhat less sharp on account of the double nature and rather varying shape of the chromosomes and this is still more the case with the diakineses.

The only stage that has been made the object of exact measurements of the chromosome dimensions is the prophase of the pollen-cell nuclei. When this prophase arrives at its climax, the chromosomes have assumed the shape of more or less cylindrical rods or — in case of the smallest ones — almost spherical bodies. As pointed out in the introduction (p. 130) the chromosomes are now generally arranged with a certain regularity, lying parallel and directed towards the pole of the foregoing (homotypic) division. Seen from this pole the chromosomes cannot, of course, be used for measurements, but in side view the dimensions can be measured with a fair degree of accuracy. Consequently the present writer arrived at the following way of performing the measurements of the chromosomes: well-fixed anthers, containing pollen-nuclei in late prophase, were looked through, and all such nuclei seen in side view and, as a rule, untouched by the microtome knife were drawn with a camera lucida at a high magnification. Afterwards the *drawings* were put under the microscope at a low magnification and length and breadth of the chromosomes were measured with an ocular micrometer.

The last-mentioned part of the method probably represents a new modification of those procedures that aim at measuring with as small errors as possible. The best way of escaping these errors is to enlarge the drawings before measuring them and this enlarging may be done in several ways. HANCE (1918) enlarged them with a pantograph and ROSENBERG (1918) used for the same purpose a projection apparatus, his drawings being made on transparent paper. The method, adopted in the present work, is simpler and can be used, as the chromosomes in the pollen-prophases are rather short and straight, the measuring with the micrometer being easy. Consequently this measuring can be done with practically negligeable error. For long and twisted chromosomes, again, the method would certainly fail.

In these chromosome measurements the following magnifications

have been used: REICH. hom. imm. $^1/_{12}$, LEITZ periplan-oc. 20 ×, the magnification thus being 2900 diameters. The drawings have then been measured with REICH. obj. No. 0, oc. 2, the enlargement thereby being further doubled. In the tables 2, 3 and 4 each unit represents one line in the micrometer and, consequently, a length of 0,017 μ in the slides. — It appears that the longest chromosomes measured are about 3,5 μ and the shortest about 0,7 μ. The species shall now be dealt with separately.

C. PILULIFERA.

This species has 9 chromosomes (haploid) of which there are 3 long (A in the following), 4 medium (B) and 2 short ones (C). These three classes can be easily recognized in the above-mentioned stages of the pollen-development (textfig. 3, Pl. I, fig. 4). Table 2 contains the lengths and breadths of the chromosomes of 34 pollen-prophases,

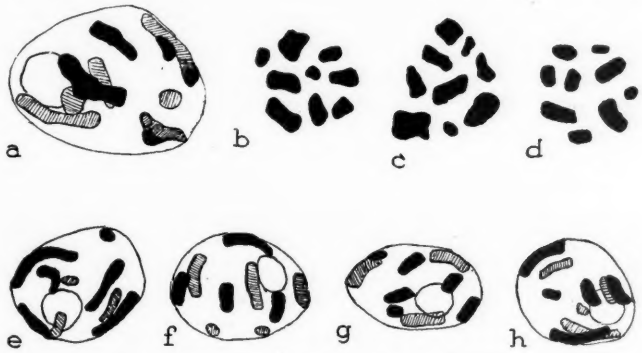

Fig. 3. *C. pilulifera.* a diakinesis in P. M. C., b—d heterotypic metaphases in P. M. C., e—h prophases in pollen-cells. — REICHERT hom. imm. $^1/_{12}$, LEITZ peripl. oc. 20 × (× 2900).

total 302 chromosomes (4 of the chromosomes having too oblique a position in the slides to be measured). Some of the figures in the table have been rounded off to even fives or tens, as the shape of the chromosomes sometimes made the measuring difficult, but this cannot visibly influence the final result.

A preliminary glance at the figures in the table shows that some nuclei contain particularly long chromosomes, whereas in others the chromosomes are, through-out, shorter. This is due to the fact that the nuclei measured had not been exactly in the same stage, the

TABLE 2. *Measurements of lengths and breadths of chromosomes in pollen-prophases of C. pilulifera. A = long, B = medium, C = short chromosomes.*

	A	A	A	B	B	B	B	C	C	A	A	A	B	B	B	B	C	C
Length	175	157	155	80	106	85	90	63	70	215	208	170	130	95	90	100	70	70
Breadth.....	55	52	47	59	44	60	60	40	45	50	50	47	40	40	40	45	38	38
Length	165	188	140	100	118	75	90	50	45	190	210	195	145	128	125	—	70	70
Breadth.....	40	45	36	30	40	45	45	40	36	45	47	45	30	45	40	—	40	36
Length	160	150	146	88	100	80	100	65	65	200	183	208	125	115	92	125	50	60
Breadth.....	40	37	38	48	38	50	48	44	29	40	35	40	35	40	50	40	40	37
Length	180	160	140	110	85	98	92	50	44	167	153	157	96	100	82	120	57	57
Breadth.....	45	33	36	40	47	40	40	35	35	45	47	46	40	42	47	48	35	35
Length	180	150	135	110	108	95	105	60	54	205	175	150	100	95	80	90	50	60
Breadth.....	45	45	50	45	42	37	46	25	37	45	40	45	46	48	35	38	32	35
Length	185	152	155	76	100	92	105	50	50	205	180	165	135	115	130	130	55	50
Breadth.....	35	30	36	46	36	45	40	30	35	35	35	47	40	30	28	35	50	40
Length	200	200	165	127	125	137	140	58	80	203	190	160	145	130	96	75	50	53
Breadth.....	35	47	36	36	30	42	35	40	38	30	35	35	35	30	30	35	36	30
Length	185	155	140	100	102	118	100	80	65	200	170	160	112	135	80	130	60	62
Breadth.....	35	36	55	34	45	35	35	30	40	45	40	35	42	32	40	46	33	35
Length	165	170	150	120	135	130	85	55	63	200	180	200	125	117	85	100	70	60
Breadth.....	40	50	45	40	37	42	40	40	32	35	37	30	40	37	35	55	42	35
Length	167	167	137	100	90	102	—	58	50	240	212	190	140	155	130	145	47	55
Breadth.....	55	60	46	58	50	54	—	35	44	40	40	40	33	35	45	38	33	35
Length	187	145	180	88	95	128	80	65	75	130	145	135	105	90	100	75	55	55
Breadth.....	45	42	43	30	70	60	50	57	40	40	44	54	46	52	40	50	36	37
Length	140	145	145	115	110	82	—	60	66	220	200	195	125	97	110	150	85	60
Breadth.....	50	55	45	43	45	56	—	40	44	50	40	40	33	35	25	42	37	43
Length	215	135	128	115	112	114	90	59	50	160	170	177	114	97	83	95	50	45
Breadth.....	45	36	40	50	45	42	40	36	40	37	45	42	40	37	30	30	35	32
Length	175	190	170	110	125	124	72	60	50	190	210	180	147	117	90	117	84	54
Breadth.....	40	38	46	47	55	35	39	36	42	40	37	46	40	35	40	33	30	40
Length	185	193	188	115	115	123	—	60	53	194	195	180	125	115	100	105	56	60
Breadth.....	40	40	38	46	32	38	—	35	35	40	47	40	30	36	45	40	30	40
Length	183	187	195	106	107	148	90	50	50	210	175	177	150	101	110	90	70	65
Breadth.....	30	40	30	37	30	42	40	25	38	45	47	50	30	42	42	43	30	45
Length	140	150	135	110	82	110	88	55	56	165	160	195	100	95	90	112	63	65
Breadth.....	35	42	33	36	32	40	45	40	27	40	45	40	47	53	38	42	38	35

chromosomes in some of them being less condensed and shortened than in others. A correction is therefore necessary to make a calcula-

tion of the size-*differences* between the three chromosome classes possible. For this purpose the writer preferred to choose the A-chromosomes as standard, these being more easily recognized in the different species and therefore better suited for comparative studies between the species. They are also — in the other species — fewer than the small chromosomes and on account of this also better suited as standards than the latter ones. Thus in each nucleus the length of the medium one of the three A-chromosomes was taken equal to 100 units and the values of the other chromosomes were accordingly calculated. It would, of course, have been more correct to take the mean value of the three A-chromosomes in each nucleus as standard, but the difference between this value and the length of the medium A-chromosome is so small as to be negligeable. The standard adopted is much simpler. The first two nuclei in table 2, for inst., gave the following corrected values:

111, 100, 99, 51, 68, 54, 57, 40, 45
103, 100, 82, 63, 46, 43, 48, 34, 34.

The corrected values for the nuclei measured are plotted in the curves, fig. 4, which represent graphically the three chromosome-

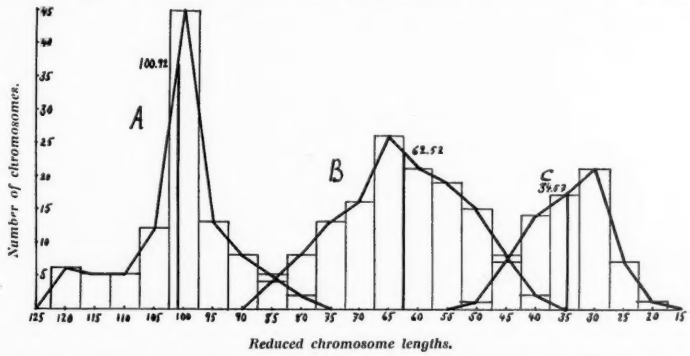

Fig. 4. Curves, representing lengths of chromosomes in *C. pilulifera* (A-, B- and C-chromosomes). Cf. text.

classes of *C. pilulifera*. The maxima are at 100, 65, and 30. The relatively great transgression between the three curves is probably due to non-simultaneity in the shortening of chromosomes within the same nucleus, for which no correction is possible, as well as to errors made during the drawing. The very excessive maximum of A depends, of course, on the unit chosen. Mean values of the lengths of the chro-

mosomes, belonging to the three classes, have been calculated and are as follows: $A = 100{,}92$, $B = 62{,}52$, $C = 34{,}57$. These values are also given in the curves.

It is seen that the sum of the lengths of B and C (97,09) nearly equals the length of A and it seems tempting to test, whether the difference found is of any importance. For this purpose the following calculation of the mean errors has been made (cf. CHARLIER 1910): $A = 100{,}92 \pm 0{,}997$, $B = 62{,}52 \pm 0{,}908$, $C = 34{,}57 \pm 0{,}748$, $B + C = 97{,}09 \pm 1{,}176$ and finally $A - (B + C) = 3{,}83 \pm 1{,}542$. It is seen that the difference between A and the sum $B + C$ is slightly less than $2\,^1/_2$ times its mean error, an agreement which is not especially good but might be regarded as somewhat satisfactory. Consequently we may state that the sum of one medium and one short chromosome is equal to one long, or $A = B + C$.

As to the breadth of the chromosomes, no attempt has been made during the measuring to distinguish between breadth and thickness, any such distinction being difficult to make. The chromosomes have been regarded as cylinders, the diameters of which are given in table 2. In reality they seem to be a little flattened. This is not, however, of any importance, because the error, thus arising, influences the figures for the three chromosome-classes equally and does, therefore, not influence the comparisons between the chromosome-classes for which, exclusively, the figures shall be used.

Further, a preliminary study of the data in table 2 shows no clear difference in chromosome breadth between nuclei with particularly long and such with short chromosomes. Hence we regard a reduction to a common unit, corresponding to what has been done with the chromosome-lengths, as unnecessary and impossible. Mean values for the three chromosome classes have been calculated directly from table 2 and are as follows: $A = 41{,}89 \pm 0{,}613$, $B = 41{,}17 \pm 0{,}671$, $C = 36{,}91 \pm 0{,}674$, further $A - B = 0{,}72 \pm 0{,}909$ and $B - C = 4{,}26 \pm 0{,}951$. These figures show that the A-chromosomes and the B-chromosomes are equally thick, the difference $A - B$ being smaller than its mean error, whereas the C-chromosomes are distinctly thinner, the difference $B - C$ being $4\,^1/_2$ times its mean error.

Summarizing our results on the chromosome set in *C. pilulifera,* we may now state that this species has 9 chromosomes (X) of which there are 3 long, 4 medium and 2 short ones. These three classes have a very simple relation to one another, the sum of the length of one medium and one short chromosome being equal to the length

of one long. If we now try to explain this simple relation or try to explain, why there should, at all, exist three classes of chromosomes, we can hardly find more than one explanation, *viz.* the following: *Either a medium and a short chromosome have arisen through transverse fragmentation of a long one or a long chromosome has, perhaps, arisen through fusion end-to-end of a medium and a short one.* The present writer holds the former alternative as the more probable, because the original chromosome set in this genus must then be supposed to have consisted of only one class of chromosomes, *viz.* long ones (A), while the latter alternative necessarily presupposes two original classes (B and C). Cf. chapt. 6.

Further, if the above-mentioned explanation is correct, it follows that all chromosomes must have the same thickness as they represent, in a certain sense, fragments of one original chromatin thread. This holds good for the long and medium chromosomes but not for the short ones which are somewhat thinner. The difference between the short chromosomes and the other ones is too great to be a matter of chance only; however, it does not seem to be so great as to make our hypothesis untenable. We might have made some special error during the drawing of the small chromosomes or, what seems more probable, there may have taken place some secondary change within the small chromosomes after the fragmenting of the original thread.

The diagram in fig. 9 gives the exact proportions of the chromosomes in *C. pilulifera.* In constructing this diagram the mean values for the chromosome lengths, derived above, have been used. As to the chromosome breadths the necessary reduction to a corresponding scale has been made in the following way: The mean value of the length of the A-chromosomes in *unreduced* units (table 2) is 174,40, the reduced or corrected value is 100,92. The reduction is to 57,87 %. Consequently, the mean values of the chromosome breadths, given above, are now reduced to 57,87 % in constructing the diagram.

C. PANICEA.

This species has 16 chromosomes (haploid) of which there are 3 long (A), 2 medium (B) and 11 short ones (C). These three classes of chromosomes probably correspond to the three classes in *C. pilulifera* for which reason the same notations (A, B and C) have been used. The three A-chromosomes can be easily recognized in all the above-mentioned stages (textfig. 5, Pl. I, fig. 5), but it is difficult from a mere inspection of the slides to determine, whether there are one,

two or perhaps more B-chromosomes and whether or not the C-class is composed of only one sort of chromosomes. A study of the measurements in table 3 shows, however, that in each nucleus there are, as a rule, two medium chromosomes. This fact also appears from the curves (fig. 6) constructed on the assumption of 2 B + 11 C and found to be in better agreement with the ideal curve than for inst. (1 B + 12 C)- or (3 B + 10 C)-curves, the latter ones being skew

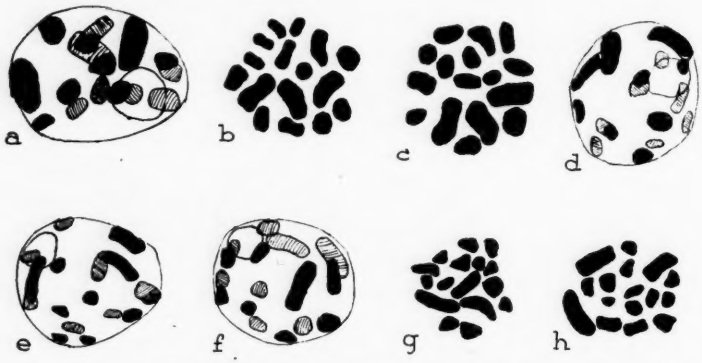

Fig. 5. *C. panicea.* a diakinesis in P. M. C., b—c heterotypic metaphases in P. M. C., d—f prophases in pollen-cells, g—h metaphases in pollen-cells. — REICH. hom. imm. 1/12, LEITZ peripl. oc. 20 × (× 2900).

or irregular. Further, the C-chromosomes give a very narrow curve with a well-marked maximum and are, therefore, most probably all of equal length.

Table 3 contains the lengths and breadths of the chromosomes of 26 pollen-prophases, total 408 chromosomes (8 chromosomes being cut off by the knife or having too oblique a position). The values of the chromosome lengths reduced from this table have been calculated in the same way as with *C. pilulifera,* the length of the medium A-chromosome in each nucleus being taken equal to 100 units. These values are plotted in the curves, fig. 6. As is seen, there is little transgression between A and B but rather much between B and C. The maxima are at 100, 60 and 40. Mean values of the lengths of the three chromosome classes have been calculated and are also given in the curves. They are: $A = 100{,}62 \pm 1{,}238$, $B = 58{,}50 \pm 1{,}226$, $C = 39{,}98 \pm 0{,}423$. Two apparently aberrant nuclei, marked with a and b in the table, have not been used in constructing these curves and in calculating the mean values. They shall be dealt with later (p. 158).

TABLE 3. *Measurements of lengths and breadths of chromosomes in pollen-prophases of C. panicea. A = long, B = medium, C = short chromosomes.*

	A	A	A	B	B	C	C	C	C	C	C	C	C	C	C	
Length	147	150	140	90	76	60	65	62	57	70	55	55	57	75	60	67	—
Breadth	50	57	55	58	60	35	38	39	38	34	36	40	50	32	31	27	—
Length	160	140	165	106	97	80	66	75	75	50	85	68	72	54	55	—	—
Breadth	60	52	45	57	47	57	35	46	50	40	58	30	53	35	37	—	—
Length	160	170	155	103	85	65	70	62	75	70	70	70	80	60	65	—	—
Breadth	60	52	50	52	70	40	35	38	35	45	40	45	53	50	50	—	—
Length	138	155	155	98	96	47	60	77	63	70	65	60	60	60	60	75	—
Breadth	64	68	45	45	50	45	45	50	47	47	45	50	48	50	45	40	—
Length	175	195	157	75	76	60	65	58	45	72	60	60	50	60	65	52	—
Breadth	61	71	52	46	45	55	40	43	35	50	40	55	37	27	42	45	—
Length	175	145	130	85	82	60	72	66	55	68	55	70	60	50	53	—	—
Breadth	46	62	54	60	35	40	42	50	55	40	37	32	40	50	37	—	—
Length	160	145	116	86	80	70	56	55	70	65	52	68	65	60	40	55	—
Breadth	45	48	40	37	40	58	52	37	43	35	37	35	42	35	40	45	—
Length	145	147	115	90	85	55	60	70	67	42	70	62	66	57	76	67	—
Breadth	40	50	75	55	42	50	50	52	47	40	58	56	40	40	55	50	—
Length	162	125	140	87	85	65	60	60	67	57	50	62	70	70	60	55	—
Breadth	38	47	40	53	53	52	40	40	47	28	40	44	37	40	30	40	—
Length	190	185	172	70	90	65	67	70	50	50	52	65	34	44	52	60	—
Breadth	50	50	47	40	45	35	35	35	37	40	35	35	35	30	34	45	—
Length	144	145	136	81	84	70	75	65	53	55	65	52	58	49	47	35	—
Breadth	35	47	54	43	37	40	40	40	35	30	32	26	36	35	35	26	—
Length	160	135	135	100	80	55	60	43	57	59	50	50	70	39	55	60	—
Breadth	60	37	44	44	37	28	30	30	35	35	40	37	30	30	32	30	—
Length	170	230	135	100	104	50	72	60	60	65	79	50	50	75	64	—	—
Breadth	50	47	50	50	22	30	44	40	45	36	45	44	40	37	37	—	—
Length	160	180	152	120	75	66	70	70	60	55	54	61	67	65	67	70	—
Breadth	55	60	57	35	45	59	40	50	45	45	40	50	42	38	50	50	—
Length	135	150	160	115	80	65	76	52	76	60	63	52	70	50	50	—	—
Breadth	51	60	55	70	46	48	43	43	45	40	42	40	55	40	35	—	—
Length	142	147	135	98	75	36	54	50	70	75	70	54	65	69	53	45	—
Breadth	40	44	40	50	41	30	40	40	37	40	35	42	46	43	35	40	—
Length	162	140	150	87	100	50	60	68	66	64	60	64	50	35	55	50	—
Breadth	60	60	62	40	36	36	39	40	50	36	43	43	38	26	36	45	—
Length	165	180	—	88	97	65	60	50	65	60	55	66	65	55	80	60	—
Breadth	50	40	—	55	35	34	44	44	30	34	39	35	43	45	42	47	—

	A	A	A	B	B	C	C	C	C	C	C	C	C	C	C	
Length	150	145	140	74	76	45	55	50	65	50	52	50	65	73	50	55	—
Breadth	32	40	42	35	40	25	44	29	32	26	40	50	30	35	40	26	—
Length	125	130	190	92	100	70	52	47	70	65	50	62	60	60	50	67	—
Breadth	45	50	60	55	45	35	30	40	50	50	35	30	40	55	38	32	—
Length	145	137	135	90	78	75	60	70	60	54	52	40	68	65	65	56	—
Breadth	50	50	60	40	40	30	35	46	34	40	36	36	35	46	40	35	—
Length	142	155	120	90	85	58	55	55	62	47	49	45	52	77	55	50	—
Breadth	55	45	55	35	44	34	35	40	34	25	35	30	40	55	30	29	—
Length	130	135	140	70	70	58	50	58	55	59	60	65	57	70	64	50	—
Breadth	45	50	50	45	47	45	40	28	30	26	45	56	55	38	55	35	—
Length	155	130	140	65	80	40	50	60	50	40	65	50	35	47	45	52	—
Breadth	26	56	54	42	38	20	28	30	25	22	42	30	30	35	30	23	—
	A	A	A	A													
Length	135	170	136	133	50	65	50	44	53	57	47	65	51	66	55	—	a
Breadth	48	50	50	45	33	60	35	30	36	44	30	26	30	31	32	—	a
Length	125	122	120	175	95	54	55	66	60	55	54	46	50	50	39	—	b
Breadth	40	40	40	34	25	35	37	35	40	42	24	25	35	33	35	—	b

It appears that $B + C = 98{,}48 \pm 1{,}297$ and $A - (B + C) = 2{,}14 \pm 1{,}793$. Thus the length of A is practically equal to the sum of B and C, the difference between A and B + C being much less than twice its mean error. We have, consequently, found the same relation between the three chromosome-classes as in the foregoing species, or $A = B + C$, and have a right to draw the same conclusion, *viz.* that the medium and short chromosomes probably have arisen through transverse fragmentation of long ones. The question as to the homology of the chromosome classes in the two species shall be discussed later (p. 152).

As in the case of the foregoing species, we must suppose the thickness of the chromosomes to be equal in the three classes, taking for granted that our hypothesis on the origin of the classes being right. Mean values of the chromosome thicknesses have been calculated from table 3 and are as follows: $A = 50{,}51 \pm 1{,}054$, $B = 45{,}46 \pm 1{,}335$, $C = 39{,}48 \pm 0{,}496$. It is seen that the agreement is not very good, the difference $A - B$ being $5{,}05 \pm 1{,}701$ or only sligthly less than three times its mean error, the difference $B - C$ being $5{,}98 \pm 1{,}424$ or more than four times its mean error and $A - C$ being $11{,}03 \pm 1{,}165$ or more than nine times

its mean error. The A- and B-chromosomes might perhaps be regarded as equally thick, while the C-chromosomes are thinner, but, as in the foregoing species, this difference does not seem to be so great as to make the hypothesis of transverse fragmentation untenable.

In fig. 9 an exact diagram of the chromosome set in *C. panicea* has been constructed in the same way as used with regard to *C. pilulifera*. As, however, the mean value of the length of the A-chromosomes in

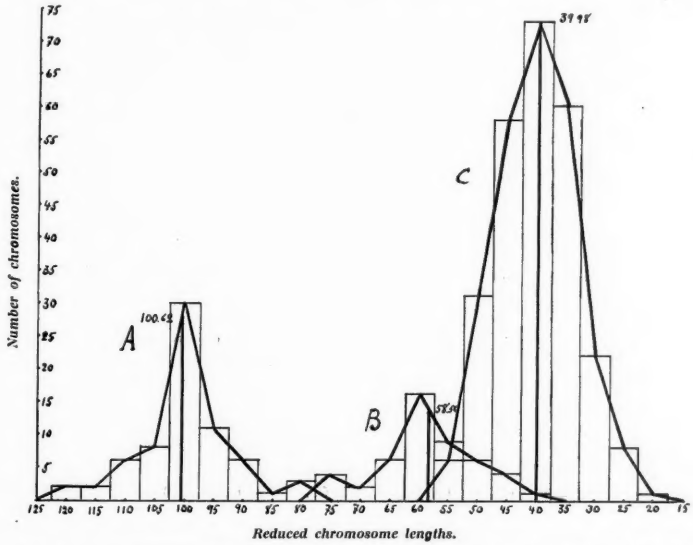

Fig. 6. Curves, representing lengths of chromosomes in *C. panicea* (A-, B-, and C-chromosomes). Cf. text.

unreduced units (table 3) is but 150,79 (174,40 in *C. pilulifera*), all figures have been once more reduced, *viz.* to 150,79 : 174,40 so that the diagram not only gives the relative sizes of the chromosomes in *C. panicea* but also makes a comparison with the foregoing (and following) species possible.

C. ERICETORUM.

This species has 15 (fig. 7) chromosomes (haploid) of which there is 1 longer and 14 shorter. For reasons developed below (p. 154), the longer chromosome should probably be regarded as a medium one (B) and the shorter chromosomes as belonging to the C-class. It is impossible to determine directly in the microscope, whether these

14 belong to only one or to several size classes, but a study of the measurements (table 4) shows the former alternative to be the more probable one. Examining each nucleus separately, we find it impossible to divide the 14 chromosomes in any smaller groups, though the shape of the curve (fig. 8) might suggest the existence of two such groups. The secondary maximum of the curve might correspond to a group of about 4 small chromosomes in each nucleus, but no such group can be maintained when each nucleus is considered separately. The secondary maximum must be the result partly of lacking simultaneity in the shortening of the chromosomes in some of the nuclei and partly of the variability in length of the B-chromosome,

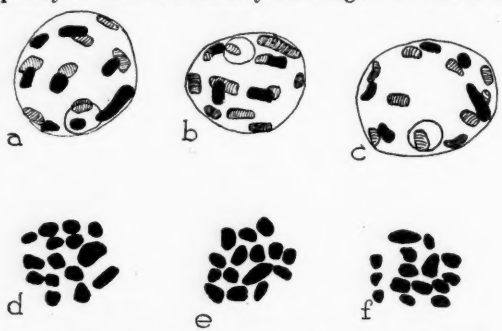

Fig. 7. *C. ericetorum.* a—c prophases in pollen-cells, d—f metaphases in pollen-cells. — REICHERT hom. imm. $^1/_{12}$, LEITZ peripl. oc. 20 × (× 2900).

used as standard at the reduction of the length values. The simultaneity of chromosome shortening is, perhaps, somewhat less in this species than in the two foregoing ones. Further it is clear, that the single B-chromosome of this species offers a much more variable standard than the medium one of the three A-chromosomes of the two foregoing species. Hence it seems almost certain that the secondary maximum would disappear, if more extensive statistics were brought together. Concluding we may state that no evidence can be brought forward to show the existence of different size classes among the 14 shorter chromosomes of *C. ericetorum.*

Table 4 contains the measurements of 265 chromosomes in 18 nuclei, 5 chromosomes being cut off by the microtome knife or having too oblique a position. As with the foregoing species, reduced values of the chromosome lengths have been calculated, the B-chromosome now being taken as standard (= 100). The values are plotted in the

TABLE 4. *Measurements of lengths and breadths of chromosomes in pollen-prophases of C. ericetorum. B = medium, C = short chromosomes.*

	B	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Length	115	110	97	60	71	62	80	57	110	66	52	80	71	81	83
Breadth	50	33	37	47	37	28	38	50	44	30	52	45	31	35	40
Length	130	80	70	85	55	63	50	70	64	70	95	62	85	43	—
Breadth	50	36	35	40	36	40	40	39	56	58	38	44	55	43	—
Length	165	60	55	50	56	66	70	70	62	65	60	70	59	68	70
Breadth	42	37	32	30	29	35	34	30	48	43	47	37	40	25	34
Length	145	70	78	68	60	60	78	64	77	60	80	81	75	73	75
Breadth	41	54	30	43	40	30	32	35	25	33	45	30	40	29	25
Length	140	52	52	50	50	50	86	70	67	82	100	75	80	82	55
Breadth	45	25	46	40	35	35	30	35	27	40	45	30	33	49	36
Length	123	62	53	95	61	75	61	45	60	63	55	90	56	60	70
Breadth	45	35	31	42	35	30	46	20	30	35	33	39	50	49	26
Length	122	80	60	75	98	80	79	85	75	80	75	74	50	66	60
Breadth	44	36	59	31	41	39	44	57	50	54	40	35	30	30	39
Length	145	71	105	70	80	80	96	96	90	63	80	—	—	—	—
Breadth	47	45	31	41	30	35	50	38	36	30	39	—	—	—	—
Length	100	71	81	71	65	86	69	76	92	50	50	90	66	75	71
Breadth	41	36	36	36	35	34	50	31	36	40	35	50	50	40	45
Length	158	90	82	55	83	75	70	90	70	90	80	59	70	50	70
Breadth	40	50	50	40	65	35	35	54	45	40	39	33	37	39	29
Length	160	80	83	90	95	85	56	67	75	70	50	90	67	80	80
Breadth	30	50	37	40	40	38	37	32	46	46	46	42	45	30	25
Length	122	70	60	75	55	70	76	91	85	90	58	90	70	75	62
Breadth	40	47	55	35	30	45	40	45	37	33	33	50	51	30	37
Length	126	75	81	70	60	75	60	50	60	65	56	70	75	80	80
Breadth	45	42	50	60	30	45	42	45	25	25	30	30	55	44	37
Length	132	105	75	58	90	70	100	95	71	75	60	76	61	82	70
Breadth	38	40	40	34	36	35	41	38	40	44	40	36	35	25	23
Length	160	43	65	60	90	60	60	60	56	62	60	60	60	50	55
Breadth	45	40	32	20	30	20	40	33	33	30	45	30	47	40	25
Length	120	50	50	52	50	64	75	65	50	81	60	58	60	63	75
Breadth	35	35	25	47	45	40	45	33	30	35	43	47	30	40	36
Length	116	112	85	75	60	60	75	66	60	51	65	90	70	66	64
Breadth	40	35	45	46	37	40	34	50	40	40	35	43	46	43	42
Length	101	83	80	75	70	92	60	80	65	66	55	66	70	55	50
Breadth	45	43	55	50	40	35	40	40	35	33	40	42	50	50	33

curves (fig. 8). The maxima are at 100 and 55. The mean value for the C-chromosomes has been calculated to $54{,}70 \pm 0{,}874$ and is, too, given in the curve. The thickness of the chromosomes (unreduced values, table 4) is $42{,}94 \pm 1{,}204$ (B) and $38{,}69 \pm 0{,}326$ (C), the difference being $4{,}25 \pm 1{,}585$. The difference is thus somewhat less than three times its mean error and the B- and C-chromosomes might perhaps

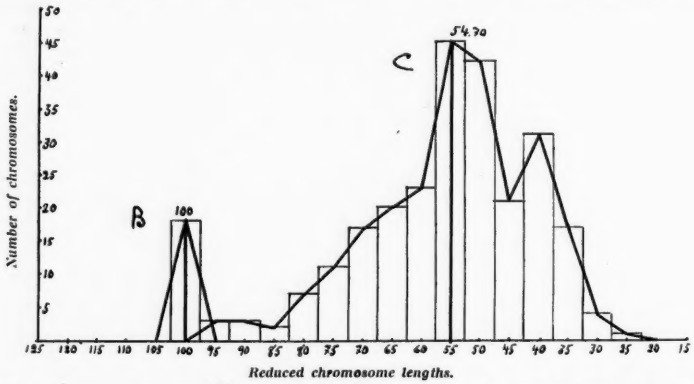

Fig. 8. Curves, representing lengths of chromosomes in *C. ericetorum* (B- and C-chromosomes). Cf. text.

be regarded as equally thick. The mean value of the unreduced lengths of the B-chromosomes is 132,22. The above figures have been used for constructing the diagram (fig. 9) in the same way as with the two foregoing species (p. 145 and 149).

COMPARISONS BETWEEN C. PILULIFERA, PANICEA AND ERICETORUM.

We have found that *C. pilulifera* has 9 chromosomes of which there are 3 long, 4 medium and 2 short ones, that *C. panicea* has 16 chromosomes of which 3 long, 2 medium and 11 short and that *C. ericetorum* has 15 chromosomes of which 1 medium and 14 short. The same notation has been used for all three species, *viz.* A for the long, B for the medium and C for the short chromosomes. This notation has been used under the assumption that the chromosomes of the three species are homologous; there now remains the task to decide, if this assumption is legitimate from a statistical point of view. We must suppose that the lengths of the chromosomes of the different classes stand in the same relations to one another in the three species, if the chromosomes are really homologous. Thus, if the

relations A : B : C are found to be the same in the three species, the assumption of homology of the chromosomes is strongly supported, though of course not proved; if, again, the relations do not agree, the homology seems less likely.

The relative chromosome lengths of *C. pilulifera* are $100{,}92 \pm 0{,}997$, $62{,}52 \pm 0{,}908$ and $34{,}57 \pm 0{,}748$, those of *C. panicea* are $100{,}62 \pm 1{,}238$, $58{,}50 \pm 1{,}226$ and $39{,}98 \pm 0{,}423$. The ratio B : A is $0{,}6195 \pm 0{,}01088$ (cf. JOHANNSEN 1913, p. 692) in *C. pilulifera,* $0{,}5814 \pm 0{,}01779$ in *C. panicea,* the difference being $0{,}0381 \pm 0{,}02085$. The ratio C : A is $0{,}3425 \pm 0{,}00815$ in *C. pilulifera,* $0{,}3973 \pm 0{,}00645$ in *C. panicea,* the difference being $0{,}0548 \pm 0{,}01039$. It is seen that the ratio B : A is about the same in both species, the difference being less than twice its mean error, whereas C : A is not the same, the difference now being more than five times its mean error. Both the long and the medium chromosomes in *C. panicea* are somewhat shorter than those in *C. pilulifera* (cf. the diagrams fig. 9), though their mutual length ratio is the same as in the latter species, the short ones, however, are of about equal length in both species. We must, therefore, suppose that the long and medium chromosomes in *C. panicea* have undergone some secondary shortening, as it is probable that *C. pilulifera* represents the more primitive condition (cf. chapt. 6). It is, however, also possible that the short chromosomes in *C. panicea* might have increased in length secondarily, as the absolute lengths are of less importance for these comparisons than the relative ones. The secondary changes, indicated above, do not, at any rate, seem so great as to make the homology between the long and medium chromosomes in *C. pilulifera* and *C. panicea* unlikely, as the length ratio B : A is equal in both species, and the short chromosomes probably are homologous too. The homology of the chromosomes in the two species is further supported by the length relation $A = B + C$, already found to hold good for both species.

The relative chromosome lengths of *C. ericetorum* are 100 ± 0 and $54{,}70 \pm 0{,}874$, these figures giving the ratio $0{,}547 \pm 0{,}00874$. Hence the difference between this value and the ratio B : A in *C. pilulifera* is $0{,}0725 \pm 0{,}01396$ and between the above-mentioned value and the ratio B : A in *C. panicea* $0{,}0344 \pm 0{,}01982$. It is seen that the relation between the shorter chromosomes and the longer one in *C. ericetorum* differs much from the ratio B : A in *C. pilulifera,* the difference being more than five times its mean error, but it appears, too, that the relation agrees, within the limits of error, with the ratio B : A in *C. panicea,* the difference in the latter case being less than twice its mean error.

On the other hand, the ratio C : B in *C. pilulifera* is $0{,}5529 \pm 0{,}01441$, the difference between this ratio and the above ratio in *C. ericetorum* thus being $0{,}0059 \pm 0{,}01685$. The ratio C : B in *C. panicea* is $0{,}6834 \pm 0{,}01605$ and the difference between this ratio and the above ratio of *C. ericetorum* is $0{,}1364 \pm 0{,}01827$. These figures show that the length ratio between the shorter chromosomes and the longer one in *C. ericetorum* is exactly the same as the ratio between the short and medium chromosomes in *C. pilulifera,* but that it differs widely from the ratio C : B in *C. panicea.* The length relation of the chromosomes in *C. ericetorum* does thus not agree with the length relations in *both* the other species. As, however, *C. ericetorum* is nearly related systematically to *C. pilulifera* and as its chromosomes show exactly the same length relations as the medium and short chromosomes do in the latter species, they should probably be homologized with the chromosomes of this species. The longer chromosome in *C. ericetorum* has therefore been characterized above as a B-chromosome and the shorter ones as C-chromosomes.

Summarizing we state that the length ratio B : A is the same in *C. pilulifera* and *C. panicea* and that the ratio C : B is the same in *C. pilulifera* and *C. ericetorum,* whereas the ratios C : A and C : B in *C. panicea* differ from the corresponding ratios in the two other species. The C-chromosomes of *C. panicea* are relatively somewhat longer than the C-chromosomes of the other species. The difference, however, is not very great and might well depend on secondary changes connected with the evolution of the species.

We thus arrive at the conclusion that our statistics on the chromosome dimensions agree on the whole with the assumption of the homology of the chromosomes in *C. pilulifera, panicea* and *ericetorum* or, in other words, that *the nuclei of these species probably contain the same sorts of chromosomes though in different numbers.* From the facts, set forth in the following, it seems probable that this holds good for the other *Carex*-species, too. As it is probable that higher chromosome numbers have arisen from lower ones (cf. chapt. 6), it follows that this increase in chromosome number must have taken place through duplication of entire chromosomes and not through transverse fragmentation. In the development of the original, fundamental chromosome set, however, the latter process has probably played a rôle, as already pointed out (p. 145).

The diagrams (fig. 9), the construction of which has been explained above (p. 145 and 149), show not only the size relations of

the chromosomes within each of the three species but also the relations between the species. They show that the short chromosomes are of about equal length in *C. pilulifera* and *C. panicea,* but that the long and medium chromosomes are somewhat shorter in *C. panicea*

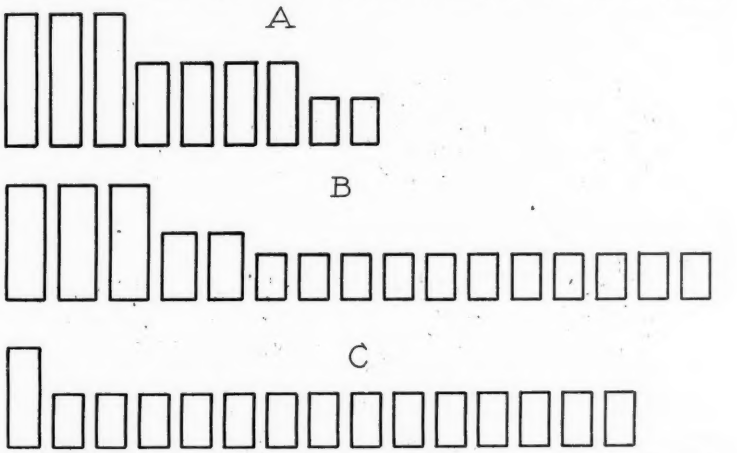

Fig. 9. Diagrams of the haploid chromosome set in: A *C. pilulifera,* B *C. panicea,* C *C. ericetorum.*

than in *C. pilulifera,* while the medium and short chromosomes in *C. ericetorum* are somewhat longer than in the two other species. This is also shown by the figures used in the construction of the diagrams which might be arranged as follows:

	A	B	C
C. pilulifera	10	: 6,2	: 3,5
C. panicea	8,7	: 5	: 3,4
C. ericetorum		7,6	: 4

It should, however, be especially pointed out that comparisons between the lengths of chromosomes in *different* species are of much less value than comparisons between the chromosomes *within one* species, as different metabolism in different species necessarily must result in different lengths even of homologous chromosomes (though not in different length relations between the size classes).

OTHER SPECIES.

In the other species no measurements have been made, because the pollen-prophases, necessary for these measurements, have, as a

rule, not been found in the slides. Examining the heterotypic metaphases, the present writer has, however, been able to analyse approximately the chromosome dimensions in a few cases (textfig. 10, Pl. I, fig. 6, 7).

In *C. sparsiflora* (X = 16) there are 2 chromosomes much bigger than the other ones and most probably homologous with the A-chro-

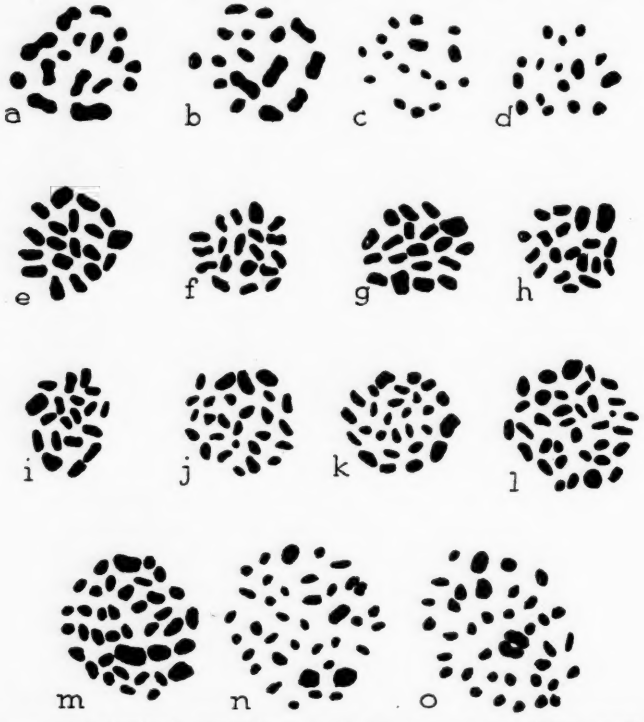

Fig. 10. a—b heterotypic metaphases in P. M. C. of *C. sparsiflora*, c—d homotypic metaphases in P. M. C. of *C. sparsiflora*, e—i heterotypic metaphases in P. M. C. of *C. montana*, j—k ditto of *C. atrata*, l ditto of *C. rigida*, m—o ditto of *C. glauca*. — REICHERT hom. imm. 1/12, LEITZ peripl. oc. 20 × (× 2900).

mosomes in the species hitherto dealt with. Among the other 14 chromosomes about 4 medium and 10 short ones can be recognized. In *C. montana* (X = 19) 2 chromosomes are distinctly bigger than the other 17, the latter apparently being of equal size, but it is somewhat difficult to decide if the two big are equal (B-chromosomes?) or if not one of them is bigger than the other and should be regarded as an

A-chromosome, while the other one might be a B-chromosome. *C. atrata* (X = 27) has probably 1 big, 2—4 medium and 24—22 small chromosomes. In *C. rigida* (X = 35) many excellent plates show 3 big chromosomes, 31 medium of about equal size and 1 very small. The figures show plates where the big chromosomes are not very clearly marked but where the diminutive one is very conspicuous. In *C. glauca* (X = 38) 4 chromosomes (A) are much bigger than the other 34. The difference between the big chromosomes and the small ones is quite as great as in *C. panicea*. *C. Hudsonii* (?, X = 40) has perhaps 2 big and 38 smaller chromosomes. Finally, according to STOUT (1913), there is in *C. aquatilis* (X = ca. 37) one chromosome distinctly bigger than the others. In some of the other species, too *(e. g. C. vesicaria),* the chromosomes seem to be of rather different sizes, though it has not been possible to classify them with any degree of certainty; in others, again *(e. g. C. digitata, Hornschuchiana),* no such conspicuous size differences are seen, the chromosome sets probably being composed of only medium and small chromosomes. It is, at least, very probable that no long chromosomes exist in these latter cases.

We may now summarize our results on the chromosome dimensions in the following list:

TABLE 5. *Chromosome dimensions in Carex.*

			X
Carex	*pilulifera*	3 A + 4 B + 2 C =	9
»	*ericetorum*	1 B + 14 C =	15
»	*panicea*	3 A + 2 B + 11 C =	16
»	*sparsiflora*	2 A + 14 (ca. 4 B + 10 C) =	16
»	*montana*	2 (B?) + 17 C =	19
»	*atrata*	1 A + (2 — 4) B + (24 — 22) C =	27
»	*rigida*	3 A + 31 B + 1 C =	35
»	*aquatilis*	1 (A?) + ca. 36 (B + C?) =	ca. 37
»	*glauca*	4 A + 34 (B + C) =	38
»	*Hudsonii* (?)	2 A + 38 (B + C) =	40

Two facts become clear from a study of this list, *viz.* that the A-chromosomes are, throughout, in the minority, the increase in chromosome number taking place among the smaller chromosomes exclusively, and that there is no constant relation between the number of chromosomes, belonging to the different size-classes, the A-chromosomes, for instance, making, in the different species, a quite different

percent of the total chromosome number. The latter fact shall be discussed in detail in chapt. 6.

IV. IRREGULARITIES IN REDUCTION DIVISION.

To be able to explain the formation of new species or forms with changed chromosome numbers it is necessary to presume the occurrence of irregularities in the reduction division or perhaps elsewhere in the life-cycle by means of which aberrant chromosome numbers arise. As such irregularities generally characterize hybrids, especially those between species or forms with different chromosome numbers, the analysis of a *Carex*-hybrid would be of great importance. Unfortunately the writer has not yet succeeded in securing material of *Carex*-hybrids, at any rate not of any hybrids of known origin (cf., however, the forms discussed on p. 136, which do not show any irregularities), but the study of the *species* has revealed a few cases of irregular chromosome behaviour in meiosis which may be of some interest (fig. 11).

In *C. pilulifera* one pollen-prophase was found with 16 chromosomes, 2 other chromosomes probably being cut off by the microtome knife. Obviously this pollen-cell had got a diploid nucleus which must be supposed to have the constitution 6 A + 8 B + 4 C. In fact, it was found to contain 4 small chromosomes, the numbers of the other ones being somewhat difficult to determine. How this diploid nucleus had arisen can not be decided, nor does it seem probable that diploid pollen-grains play any great rôle in the evolution of new species of *Carex,* as there is no polyploidy to be found in this genus (cf. chapt. 6).

In *C. panicea* 36 perfectly good heterotypic metaphases have been counted, 35 of them having 16 chromosomes but one having 17 of which 4 big and 13 smaller ones. Obviously the two big chromosomes that are seen lying together in the plate (fig. 11 b) are univalents, belonging to the same pair and both lying in the equatorial plane on account of lacking conjugation. About their behaviour in the divisions we know nothing, but, as they lie in the equatorial plane, it is very probable that they would have divided at least in the first division, perhaps in both, and given rise to a pollen-grain with 17 chromosomes. This presumption is supported by the two pollen-prophases in fig. 11 c—d which both have 4 long chromosomes. Unfortunately both have been cut by the knife and do not show more than 15 chromosomes each, so it is impossible to decide, if they really

have contained 17 chromosomes, a presumption which is extremely probable however. The measures of the chromosomes in these nuclei are found in table 3 (a and b). If the medium one of the three biggest chromosomes is taken as standard (= 100), as has been done with the other

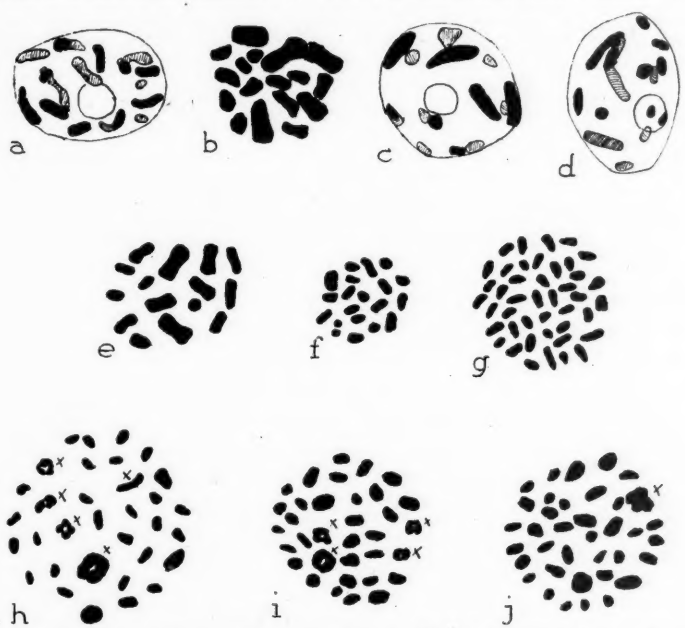

Fig. 11. Irregularities in meiosis: a prophase in diploid pollen-nucleus of *C. piluli-fera*, b heterotypic metaphase in P. M. C. of *C. panicea* with 17 chromosomes, of which 4 long, c prophase in pollen-cell of *C. panicea* with 4 long chromosomes (a in table 3), d ditto (b in table 3), e heterotypic metaphase in P. M. C. of *C. sparsi-flora* with apparently only 15 chromosomes, f heterotypic metaphase in P. M. C. of *C. montana* with 20 chromosomes, g ditto of *C. Goodenoughii* with 43 chromosomes, h—j heterotypic metaphases in P. M. C. of *C. glauca* with apparently 33, 34 and 37 chromosomes resp., chromosomes marked with X being composed of two gemini each. — REICHERT hom. imm. 1/12, LEITZ peripl. oc. 20 × (× 2900).

nuclei of this species, the lengths of the chromosomes get the following values:

125, 100, 99, 98, 48, 48, 48, 42, 40, 39, 38, 37, 37, 35, 32 a

140, 100, 98, 96, 76, 53, 48, 44, 44, 43, 43, 40, 40, 37, 31 b.

If these values are compared with the curves (fig. 6), it is seen that the smallest of the big chromosomes falls, in both cases, very near the maximum of the A-curve and far from the upper limit of

the B-curve. This means that, very probably, all the four big chromosomes belong to the A-class and that the two pollen-nuclei have the constitution 4 A + 2 B + 11 C = 17. Apparently they have arisen from an aberrant metaphase of the kind described above. As one aberrant heterotypic metaphase has been found among 36 and two aberrant pollen-prophases among 26 (table 3), these irregularities do not seem to be any rare occurrences.

In a slide of *C. sparsiflora* many heterotypic metaphases were found with only 15 chromosomes of which 2 were long and probably 4 medium and 9 small. Among these 15-chromosome metaphases several 16-chromosome metaphases, too, were found. Later 16 was found to be the normal number in this species. The writer regards it as probable that the number 15 had arisen through a rather loose attachment of a small chromosome to one of the others, probably no real fusion taking place between the two chromosomes. It seems quite excluded that any pollen-grains with aberrant chromosome numbers could arise in this way. It is probable that the attached 16:th chromosome is always a small one and always attached to the same one of the other chromosomes, these two chromosomes showing some sort of affinity to one another.

A quite similar case was later found in *C. glauca* (X = 38), where many excellently fixed metaphase plates in the heterotypic division were found with, apparently, only 33, 34, 35, 36 and 37 chromosomes. A close examination of these plates showed that some of the chromosomes were rather conspicuously double, often tetrad-like (marked with a X in fig. 11). When such tetrad-like chromosomes — not else occurring in this genus — were counted as two each, the haploid number 38 was always attained. It is obvious that some gemini have here as well as in *C. sparsiflora* a special affinity to one another which probably depends upon homology and results in a lose union to a sort of double gemini or »quadrivalents». The interesting thing in these cases is that they show the existence of homologous gemini that must have arisen through duplication (cf. p. 180).

In *C. montana* 23 perfectly clear heterotypic metaphases had 19 chromosomes, while one had 20, two of the chromosomes in the latter plate being very small and probably having arisen through lacking conjugation or through fragmentation in the middle of a dumbbell-shaped chromosome. The dumbbell-shape is very common in the heterotypic metaphases in this genus and offers perhaps opportunities for transverse fragmentation of chromosomes. This question shall be

further discussed in chapt. 6. — In *C. Goodenoughii* 19 very good heterotypic metaphases had 42 chromosomes and 1 had 43. The extra chromosome had, probably, arisen in the same way as in the foregoing species.

V. RELATIONS BETWEEN CHROMOSOME NUMBER AND SYSTEMATIC POSITION OF THE SPECIES.

Relations between chromosome number and systematic position have been found in several cases, among plants as well as animals, most of these cases having been analysed during the last few years. The problem of the systematic value of the chromosome numbers is a rather new one and very much still remains to be done, before any general statements can be made, but in the study of smaller systematic groups much information may be obtained, already now, from the chromosome numbers. TISCHLER says (1916, p. 204): »Also mit dem Anschneiden der grossen phylogenetischen Probleme auf der Basis der Chromosomenuntersuchungen ist es wohl noch zu früh. Wohl aber meine ich, dass wir auch jetzt schon die Chromosomenzahlen verwerten können, wenn wir die Gattungen oder gar die Species mit verschiedenen Zahlen ins Auge fassen.» — Some of the most significant cases, hitherto investigated, are reviewed in the following.

In *Triticum* SAKAMURA (1918, 1920) and SAX (1921, 1922) found one species with 14 chromosomes (2 X), four species with 28 and three with 42 chromosomes. The 14-chromosome species is the one-grained *T. monococcum,* the four 28-chromosome species belong to the emmer wheats and the three 42-chromosome species (among which *T. vulgare*) belong to the spelt wheats. From this SAKAMURA and SAX conclude that the one-grained wheats are the primitive ones, from which the emmer and spelt wheats have arisen, a view found to be quite in accord with the results on the phylogeny of these species, arrived at by other authors, through studies on their morphology, rust resistance, serological relations and mutual fertility or sterility. — MARCHAL (1920) investigated *Campanula* and found in the section *Medium* fifteen species with 17 chromosomes (X), two species with 34 and one with 51 chromosomes, consequently eigtheen species with $X = 17$ or a multiple of this figure, while one species was found with the exceptional figure $X = 10$. On the other hand, of seven species out of the section *Rapunculus* three had 8, two had 10, one 13 and one 17 chromosomes, this section thus being less homogeneous and

probably more primitive, too. — In *Primula* MARCHAL and other authors (cf. MARCHAL 1920 and DAHLGREN 1916) found four species or races with X = 9 and 18 in the section *Floribundae,* two species with X = 9 and 11 in the section *Farinosae,* four species or races with X = 12 and 24 in the section *Sinenses* and one species with X = 27 in the section *Auriculae.* — In *Lactuca* ISHIKAWA (1921) found a very interesting distribution of the chromosome numbers on the different subgenera. Thus five species of the subgenus *Lactuca* (in a limited sense) had 9 chromosomes (X), four of *Crepidiastrum* had 5 and three of *Paraixeris* had 5, while nine of *Ixeris* showed the series 7, 8, 12, 16 and 24. The shape of the chromosomes, too, was somewhat different in the different groups. — In *Rosa* TÄCKHOLM (1920, 1922) states that all species, belonging to the section *Caninae* (57 species, subspecies and varieties of this section investigated) are apomictical hybrids with 7 bivalent and 14, 21 or 28 univalent chromosomes, whereas the (wild) species that belong to the other sections are not hybrids and have 7, 14, 21 or 28 as haploid chromosome numbers. Some of the last-mentioned sections have species with only 7 or only 14 chromosomes, others contain both 7- and 14-chromosome species and *Cinnamomeae* consists of species with all four numbers. It is interesting to note that among the 7-chromosome sections several monotypic or very small, Asiatic groups are found as well as the great wide-spread though preponderatingly Asiatic and subtropical section *Systylae,* while the high chromosome numbers are limited to the great circumpolar, partly arctic or montanic section *Cinnamomeae.* Additional information on the cytology of the different *Rosa*-groups is found in the work of BLACKBURN and HARRISON (1921). — In *Viola* according to MIYAJI (1913) and MARCHAL (1920) one species of the subgenus *Dischidium* has X = 6, while seven species of the subgenus *Nominium* have X = 10, 12, 24 and 36. In this last-mentioned case it seems difficult, however, to find any clear relations between chromosome number and systematic position.

In a few additional plant genera rather many chromosome numbers are known, but the investigators have not tried to group the numbers according to systematic relationship of the species and have, consequently, not been able to draw any conclusions of interest in this connection. Of these genera *Chrysanthemum* (TAHARA 1915 and 1921) seems especially promising for an investigation of the kind here dealt with. The present writer has, therefore, tried to classify the species, the chromosome numbers of which TAHARA has determined to 9, 18,

27, 36 and 45, according to the system adopted in ENGLER and PRANTL's *Pflanzenfamilien,* and has arrived at the following result. Two species of sect. *Pinardia* have X = 9, one of sect. *Ismelia* has 9, one of sect. *Coleostephus* has 9, while a number of species belonging to sect. *Pyrethrum* show all the above-mentioned numbers. Hence it appears probable that the three first-mentioned sections, that are small ones, are more homogeneous as to chromosome number than the very great sect. *Pyrethrum.* The writer has not tried to make any classification of the species within this last-mentioned section.

It should be added that WINGE (1917) expressed the opinion that all *Anthemideae* of the family *Compositae* have chromosome numbers that are multiples of 9, while the numbers of *Heliantheae* are multiples of 8. The present writer is, however, not of the opinion that this conclusion is well founded, as the material investigated is too scanty.

In the animal kingdom, too, some cases are known, where relations between chromosome numbers and systematic position can be found. Thus BRAUN (1909), MATSCHEK (1910) and other authors (cf. KORNHAUSER 1915) investigated the genus *Cyclops* and counted the chromosomes of several species. They found the chromosome numbers in this genus ranging from 2 to 11 (haploid), nearly related species, however, generally having the same or adjacent numbers. If the species are arranged in groups according to their phylogenetic relationships, we get the following groups of adjacent chromosome numbers: 11 and 11; 9, 9 and 6; 9 and 7; 7 and 7; 7, 7, 6 and 6; 7 and 6; 6, 5, 5, 5 and 2; 6 and 3. The agreement is seen to be fairly good. The authors are of the opinion that the low numbers have been developed from the high ones which are thus regarded as more primitive. The comparative study of several morphological characters shows this to have been the probable course of the evolution (according to the above-mentioned authors). In *Carex,* again, the evolution has probably gone in the reverse direction, from low numbers to high ones (p. 185), and, as appears from the discussion in chapt. 6, the same seems to have been the case with most plant genera and some animal genera, too.

That chromosome numbers may be important factors in taxonomy has been concluded by several zoologists, by MONTGOMERY already in 1906 (MONTGOMERY 1906), later especially by MCCLUNG. MCCLUNG and his collaborators have mainly studied certain Orthopteran groups and have found a remarkably uniform constitution of

the chromosome sets within these groups, especially in the family *Acrididae*. According to McCLUNG (1923) »the outstanding fact which has been revealed by this study of practically all of the genera of North American Acrididae is that the entire family possesses a characteristic chromosome complex, the most marked feature of which, in nearly every case, is a common number». This number is 24 in the females, 23 in the males (diploid). Moreover, the chromosomes »occur in an approximately like size seriation, ranging through proportionately equal steps from the smallest to one five to ten times its size». This gradation from the smallest to the largest chromosome is always found and indicates that the nuclei of the whole group have essentially the same constitution, the chromosomes in the different species probably being homologous. In some species or genera differences in chromosome number are found, but this numerical variation is found to be due, principally, to a more or less temporary fusion between certain chromosomes, especially the largest members of the complex. This formation of multiple chromosomes, as well as certain differences in chromosome shape, often constitute distinct *generic* differences.

The Orthopterans thus offer an interesting example of a group, where the chromosome sets are found to be of taxonomic value for whole genera and families. Mrs. HARVEY (1916, 1920) finds in a study on chromosome numbers in *Metazoa* that a »type number» may be established for all larger groups, this number being more frequently occurring than any other numbers and being the fundamental number from which the other ones probably have arisen. Instances of such type numbers, given by mrs. HARVEY, are (haploid) 18 for *Echinodermata,* 16 for *Annelida,* 8 for *Crustacea,* 10 for *Coleoptera,* 31 for *Lepidoptera,* 12 for *Amphibia* and so on. To the present writer it seems, however, very doubtful, if any such type numbers really can be established as a general characteristic of so large groups. In some groups a type number probably may be maintained, *e. g.* 12 (haploid) in the *Acrididae,* but in others the variation in chromosome numbers seems to be far too great as to admit of any such generalisations. Groups of the last-mentioned kind are (cf. HARVEY 1920) *Nematoidea* with X ranging from 1 to 24, *Aphidae* with $X = 3 - 20$ or *Copepoda* with $X = 2 - 17$.

In higher plants it seems, at least at present, quite impossible to find any such type numbers, characteristic of larger groups (cf. chapt. 9). If we, however, wish to classify species within a genus or

to trace the phylogenetic relationships between species or groups of species in a genus, we may often find a clue in the chromosome numbers. This is clearly seen in the above review of botanical cases. In some of these cases, where multiple chromosome numbers are found, it is thus seen that nearly related species have the same chromosome number *(Triticum, Rosa).* In other cases, again, different sections of a genus are characterized by different series of, as a rule, multiple numbers, related species consequently belonging to the same series *(Campanula, Primula, Lactuca).* The *Caninae*-section of the genus *Rosa* offers a quite special case.

Finally it should be pointed out that all evidence, hitherto brought forward in plants as well as in animals, shows the chromosome number of a given species to be a constant. It is certain that exceptions occur from this rule, but these exceptions — at least those that are safely established — are rare.

Proceeding to the genus *Carex,* we now set up the following two questions to be answered, *viz.* 1) whether the last-mentioned rule of constancy in the chromosome number of a species holds good for this genus, too, and 2) whether any relations are to be found between the chromosome numbers and the taxonomy of the genus.

A study of the first question might seem to be rather unnecessary, but, as the chromosome numbers in *Carex* are so exceptionally variable and irregular, we have found it necessary to test, whether really a species of this genus has the same chromosome number in different localities, even in those situated far from one another. The following few instances investigated (cf. table 1) show that this is the case.

Thus individuals of *C. sparsiflora* from two localities, Fjällnäs in Sweden and Valdres in Norway, have been investigated. From both localities the material showed 16 chromosomes. Material of *C. gracilis* from Uppsala and from Stockholm showed 42 chromosomes, the former with perfect clearness, the latter with the greatest probability at least. A similar result was found in *C. atrata.* In this species the haploid number had already been determined to 27, when the writer undertook an investigation of a specimen in Hort. Berg., labelled *C. alpina* × *atrata* (?), though it looked rather like a typical *C. atrata.* If it really were a hybrid, it must probably belong to the F_1-generation and show at least 28 chromosomes in the heterotypic metaphases (27 bivalents and 1 univalent), but, in fact, it showed only 27. Thus it was apparently a pure *C. atrata.* It had been collected on Hamrafjället, a mountain in the province Härjedalen, Sweden. The origin of

the other material of *C. atrata* investigated is not known, but probably it had not been collected at quite so remote a place. Anyhow, both specimens examined showed X = 27. Finally *C. lepidocarpa* has been investigated from two localities, one in the province of Scania and one on the island Gotland in south Sweden. The material from both localities showed clearly 34 chromosomes.

It thus appears that in all the above instances the chromosome number of a species is the same in different localities.

As to the second question — relations between chromosome number and systematic position of the species — a study of table 1 shows such relations to exist. An examination of all those sections of the genus, where the chromosome number of at least two species have been determined, shows that *species, belonging to the same section, have numbers of about the same height.* Table 6 shows clearly that *groups of adjacent chromosome numbers are obtained, when the species are arranged according to systematic relationship.* This holds good especially for the two best-known groups, *Acutae* and *Spirostachyae,* but for the other ones, too, though in a few cases the numbers do not agree so very closely. Ca. 37 in *Atratae,* 9 in *Montanae,* 28 in *Spirostachyae* and 26 in *Physocarpae* are such instances of somewhat differing numbers. It should, however, be pointed out that *Montanae* probably is no very homogeneous group, and that the somewhat aberrant species in *Physocarpae* belongs to another subsection than the two other species investigated. The two species of *Pachystylae* do not agree very well either, but this section is perhaps not a quite »natural» one.

TABLE 6. *Systematic distribution of the chromosome numbers in Carex.*

	X
Sect. *Muehlenbergianae*	29, ca. 29
» *Acutae*	
Subsect. *Rigidae*	35
» *Vulgares*	ca. 37, 42, 42, ca. 42
» *Caespitosae*	40, 40
Sect. *Atratae*	27, 28, ca. 37
» *Pachystylae*	24, 32
» *Montanae*	9, 15, 19
» *Digitatae*	ca. 23, 26
» *Paniceae*	16, 16
» *Spirostachyae*	28, 33, 34, 34, 35, 37

Sect. *Physocarpae*
Subsect. *Lupulinae* 26
» *Vesicariae* 38, 41

It is thus clear that in the genus *Carex* nearly related species possess the same or adjacent chromosome numbers, this genus, consequently, showing a relation between chromosome numbers and taxonomy similar to that, already found in the genus *Cyclops*. This relation was observed in *Carex* by the present writer several years ago and every new number, since then determined, has proved to agree more or less closely with those previously known in the same section. In other words, it has been possible to *predict* approximately the number of a certain species, when the number of some related species was already known. This is a fairly good proof of the validity in this genus of the relation between chromosome numbers and systematics, outlined above. Moreover, as this relation has been found to hold good in all cases, hitherto investigated, it seems allowable to convert the thesis and to state that *the chromosome numbers of a group of related species may be approximately estimated, when the number of one species of the group is known.*

As some sections are seen to have low numbers *(Montanae, Paniceae),* others very high *(Acutae, Physocarpae vesicariae, Hirtae),* it appears very probable that the chromosome numbers may be of importance in the classification of the genus and in tracing its phylogeny. The last-mentioned problem shall be dealt with in chapt. 8.

VI. ORIGIN OF THE CHROMOSOME NUMBERS IN CAREX.

In the following an attempt shall be made to combine all the facts, brought together in the preceding chapters, in such a way as to throw some light on the problem of the origin of the chromosome numbers in *Carex*.

Two facts, stated in chapt. 2 and 3 (p. 137 and 157), should first be borne in mind, *viz.* that the chromosome numbers in this genus are quite irregular and that no fixed relation, constant for all species, can be found between the number of chromosomes of the different size classes. From this may be concluded that *no polyploid species exist in this genus,* a conclusion, already drawn in the writer's preliminary note (HEILBORN 1922) and pointed out in the introduction to the present paper (p. 132).

It is of importance now to define somewhat more clearly the meaning of the word polyploid. It appears from the list of chromosome numbers in chapt. 2 that there are several numbers that constitute, apparently, a series of multiples with 3 as the fundamental number (9, 15, 24, 27, 33, 36 and 42), others, again, that form a series with 4 as fundamental number (16, 24, 28, 32, 36, 40 and 56), others with 7 (28, 35, 42 and 56) and so on, but, according to the author's opinion, these merely arithmetical relations cannot be regarded as cases of polyploidy. The chromosome group of a polyploid species must necessarily contain a certain number of complete haploid chromosome sets and it must have arisen through addition of such sets. We know, however, that, for instance, *C. pilulifera* does not contain 3 sets of 3 chromosomes but 3 long, 4 medium and 2 short chromosomes, that *C. ericetorum* does not contain 5 such sets but 1 medium and 14 short chromosomes and that, consequently, the chromosome groups in these two species have not arisen through an addition of such sets but in some other way. The present writer cannot agree with WINKLER (1920, p. 165 ff.), according to which the word polyploidy should be used in a merely arithmetical sense, referring exclusively to the relation of chromosome *numbers* (»ausschliesslich im Hinblick auf die Zahlenverhältnisse zu gebrauchen und andere (Ausdrücke) anzuwenden, wenn man aussprechen will, dass der haploide Chromosomensatz — — — mehrfach vorhanden ist»). It seems absurd to the present writer to characterize a species as *C. atrata* with 27 haploid chromosomes as polyploid, *e. g.* compared with *C. pilulifera,* as the chromosome group of the first-mentioned species has, most probably, arisen through some process of duplication of *single* chromosomes (cf. p. 181), the result of this process being a group, containing 1 big, 2—4 medium and 24—22 smaller chromosomes and, consequently, not containing three sets of 9 chromosomes. WINKLER says: »Polyploid nennen wir einen Organismus, der in seinen Kernen eine Chromosomenzahl besitzt, die ein Vielfaches der haploiden Zahl darstellt.» But what is in *Carex* the haploid number? And can we regard it appropriate to speak of a multiple number, when there has, probably, never taken place any multiplication? The idea of a multiplication of a fundamental number seems to the present writer inseparable from the word polyploid. This word should be used in analogy with the words haploid and diploid which refer to the two cytological phases in the development of animals and plants.

Perhaps did WINKLER in his definition not quite realize the possibility of a case like *Carex*.

To characterize a species, containing a chromosome group of several complete haploid sets, WINKLER uses the word polygenomatic. The genoms or haploid sets may be »gleichartig» (identical from a genetical point of view?) or not (homo- or heterogenomatic nuclei, cells and organisms), and may consist of the same number of chromosomes or of different numbers. These distinctions are of theoretical interest but seem to be of rather little practical value. How should it be possible to determine, whether a species is homo- or heterogenomatic or, if the genoms contain different numbers of chromosomes, whether it is polygenomatic at all?

The present writer prefers to use the word polyploid in the same sense as WINKLER uses the word polygenomatic, provided that the genoms or haploid sets contain the same chromosome number. A polyploid species should thus be a species, the nuclei of which contain a multiple of haploid sets, all with the same number of chromosomes, though it is not necessary that these sets should be identical from a genetical point of view.

Since the above lines were written, the author came across the recent paper by BLAKESLEE, BELLING and FARNHAM (1923) on tetraploid *Daturas,* in the introduction of which opinions are expressed as to the use of the word tetraploid that agree with the views expressed in this paper. The above-mentioned authors say: »Tetraploid is a term applied to a doubling of the number of chromosomes in the constituent cells of a plant or animal. By some writers — — — a species which has twice as many chromosomes as a closely related form is called tetraploid. The writers, however, feel strongly the desirability of confining the term to a doubling of homologous chromosomes — — —. In the narrower sense in which we shall use the word, therefore, a tetraploid plant will have in each somatic cell four homologous chromosomes in each chromosomal set, whereas a diploid plant has but two and a haploid plant — — — or haploid stage has but one in each set. The mere fact that a plant has twice as many chromosomes as a related form, although affording presumptive evidence, will not of itself justify one, we believe, in calling it tetraploid. — — — Before the term tetraploid can properly be applied, therefore, there must be evidence from the cytology or from the breeding behaviour to indicate that the increase in number has been brought about by a doubling of the homologous chromosomes in each set. That a mere

numerical count of the individual chromosomes may not enable us to classify properly a plant is shown by the fact that we have found individuals of *Datura* in which the presence of an extra chromosome in one set was numerically compensated by a deficiency in another set. Thus, of two plants — — — each of which had a total of 48 chromosomes in their somatic cells — — —, one appears to have been — — — of the type (4 n + 1 — 1) and the other — — — (4 n + 1 + 1 — 1 — 1). Such forms obviously cannot properly be called 4 n or tetraploid. They — — — may be classified as modified tetraploids, or at most as 'pseudotetraploids'.»

The present writer wishes to point out that the difference between the 4 n and the (4 n + 1 + 1 — 1 — 1) types is an analogy to the difference between *C. panicea* with 3 A + 2 B + 11 C = 16 and *C. sparsiflora* with 2 A + 4 B + 10 C = 16 chromosomes. GATES, too, in a recent paper (1924) on polyploidy, uses this word apparently in the same sense as the present writer. In this sense of the word polyploidy does not occur in the genus *Carex*. This was already stated above and shall now be explained somewhat more in detail.

If the haploid chromosome group of an organism consists of a certain number of size classes, the classes containing, for inst., 3, 4, 6 and 7 chromosomes resp., the diploid group consists of the same number of classes, but the classes now contain the double number of chromosomes, *viz.*, in this case, 6, 8, 12 and 14 resp. SUTTON (1902) was the first to state this fact in *Brachystola* and it has since then been confirmed in many cases. From this fact may be concluded that, if a genus contains species, the chromosome groups of which are composed of complete haploid sets, the same size classes must reappear in all the species and the number of chromosomes in the classes must be proportional to the number of haploid sets in the species. Take it for granted that we have a genus with the chromosome numbers 9, 18, 27, 36, 45 and that the 9-chromosome species contain 3 long, 4 medium and 2 short chromosomes, then we must expect the 18-chromosome species to contain 6 long, 8 medium and 4 short chromosomes, the 27-chromosome species to contain 9 long, 12 medium and 6 short ones and so on. Such relations have really been proved to exist in some cases during the last few years.

Thus ROSENBERG (1917) found in several species of *Hieracium* with the haploid numbers 9 and 18 that the last-mentioned species contain the double number of chromosomes of each size class as compared with the 9-chromosome species. The 18-chromosome spe-

cies must, therefore, be regarded as tetraploid. In *Crepis* the same author (1920) found 7 long, 7 medium and 7 short chromosomes in a species with X = 21 and, as species with X = 3 have 1 long, 1 medium and 1 short chromosome, he regards the first-mentioned species as 14-ploid. That the chromosomes of *Crepis*-species keep their relative sizes in hybrids, together with chromosomes of other species or surrounded by a foreign plasma, may be concluded from the recent work by COLLINS and MANN (1923) and supports strongly the view that chromosome relations of the above-mentioned kind may be taken as a proof of polyploidy. SAKAMURA (1920) states that *Vicia cracca* has 12 somatic chromosomes of which 2 are very long with a constriction near the end, while *V. unijuga* has 24 somatic chromosomes of which 4 are very long with a constriction near the end. The latter species is regarded as tetraploid.

In the following cases the size relations of the chromosomes indicate the existence of triploid forms. STOMPS (1919) found in *Narcissus poeticus* 16 somatic chromosomes of which two of each size, in *Narcissus biflorus* 24 somatic chromosomes of which three of each size. The latter species is regarded as a triploid hybrid. OSAWA (1920) investigated several species and races of *Morus* and found that some have 28 somatic chromosomes of which 2 were much longer than the other ones, whereas some races have 42 somatic chromosomes of which 3 very long ones. These latter races must be triploid. DE MOL (1921) found that many races of *Hyacinthus orientalis* have 16 somatic chromosomes of which 4 short, 4 medium and 8 long ones. Some other races, again, have 24 chromosomes of which 6 short, 6 medium and 12 long ones and should, therefore, be regarded as triploid.

Finally it should be mentioned that BELLING among the different mutants of *Datura stramonium*, investigated by him, BLAKESLEE and others, has found some with the somatic number 36 and others with 48, while the normal type has 24 (cf. BELLING 1923). In the reduction division there are six size classes to be distinguished among the 12 bivalent chromosomes of the normal plant, *viz.* 1 largest, 4 large, 3 medium, 2 small medium, 1 small and 1 smallest. In the triploid and tetraploid mutants these size classes reappear but now contain trivalents, resp. quadrivalents.

It is thus seen that in species with multiple chromosome numbers and distinct differences in chromosome size, the number of chromosomes, belonging to a certain size class, in all cases hitherto investigated, is exactly proportional to the number of haploid sets, supposed

to be contained in the chromosome group of the species. From this we conclude that, if we want to test, whether a genus contains polyploid species (in our sense of the word), we have to determine the chromosome numbers of the species and to investigate the relations between the size classes in which the chromosomes eventually might be divided. If the chromosome numbers are found to form a series of multiples and the relations between the size classes agree with the facts, stated above, we may conclude that polyploidy occurs in the genus; if, again, no multiple numbers occur, or if the size classes do not stand in any fixed relation to one another, polyploidy does not occur in the genus.

How do now these matter stand in the genus *Carex*? As was seen in chapt. 2, the chromosome numbers in this genus are quite irregular, at least twenty-two different numbers having as yet been found, ranging from 9 to 56. Some of them might be arranged in a series with 3 as fundamental number, others in a series with 4 as fundamental number and so on, but no fundamental number, common for the whole genus, can be established. It is, moreover, very unlikely that more than one series of multiples should occur within this genus, because nearly related species must then often be referred to different series. There is, however, a possibility that the irregular numbers in this genus might have arisen secondarily from an original series of multiples. If this should be the case, one must expect some vestiges of the original series still to exist. One might presume that numbers in the neighbourhood of the original multiples should be more numerous than other ones or that nearly related species, probably descending from a common ancestor with a multiple number, should have numbers, grouping themselves round the number of the ancestral species. Neither of these presumptions are, however, found to hold good.

The accurately determined chromosome numbers in *Carex* may be arranged in the following way that shows their relative frequency:

TABLE. 7. *Frequency of chromosome numbers in Carex.*

Number of chromosomes	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Number of species or forms	1	—	—	—	—	—	1	2	—	—	1	—	—	—	—	1	1
Number of chromosomes	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Number of species or forms	3	3	3	1	—	1	2	2	3	2	1	1	2	—	2	1	2

56
1

As is seen, the table gives no indications of any original multiple numbers. A study of table 6 (p. 166), where the numbers are arranged according to systematic relationship of the species, gives the same negative result. We may state that not the slightest vestiges of a series of multiple chromosome numbers are to be found in this genus. The numbers are quite irregular.

As to the size classes, it has already been stated in chapt. 3 (p. 157) that there is no constant relation to be found in this genus between the number of chromosomes, belonging to the different size classes. This fact has been further pointed out in the beginning of the present chapter. — From the irregular chromosome numbers and the irregular numerical relations between the size classes we may now once more conclude that *polyploidy* (in our sense of the word) *does not occur in the genus Carex*.

The hypothesis of WINGE (1917), worked out to explain the development of multiple chromosome numbers, is, consequently, of no use in this case. We must seek for some other explanations.

The possibility of transverse division of chromosomes shall at first be discussed. Such transverse divisions have been repeatedly reported by several authors, but most of these data are very inaccurate and of little value. There is, in fact, not the slightest ground for the hypothesis of STRASBURGER (1910) that transverse division of chromosomes should occur in such cases, where increase in chromosome number is accompanied by decrease in chromosome size. As an example of such presumed transverse divisions may be cited the *Primula*-hybrid, investigated by FARMER and DIGBY (1914). Of this hybrid there were two kinds of individuals found, some with 9 and others with 18 chromosomes (haploid). The volume of a chromosome of the second kind of individuals is only half of that of a chromosome of the first kind. From this fact the conclusion was drawn that two chromosomes of the 18-chromosome individuals should be regarded as equivalent to one of the 9-chromosome individuals arising through transverse division of one of the last-mentioned. This conclusion is most certainly incorrect. To the present writer the correct explanation seems to be, simply, that there is a limit in the cells' capacity of producing chromatin, which causes the decrease in chromosome size. This explanation is the one set forth concerning *Carex* in chapt. 3 of this work.

On the whole there seems to be, in most of the accounts of transverse divisions, especially the older ones, a misunderstanding as

to the nature of such divisions. The authors seem to be of the opinion that a transverse division may occur in all the chromosomes of a nucleus simultaneously, just as the longitudinal divisions do. They do not seem to realize that longitudinal divisions are regular occurrences in the developmental cycle of the cells and that all chromosomes have the same possibilities, in their constitution, for longitudinal divisions, whereas transverse divisions must be regarded as rather exceptional and not occurring under the same circumstances in different chromosomes. We now know from the *Drosophila*-investigations that different chromosomes may have a very different constitution and that there is a linear arrangement of the genes within the chromosomes, the different parts, too, of the same chromosome having a different constitution. This is confirmed by several morphological observations, *e. g.* on chromosomes of different sizes and on constrictions in certain parts of the chromosomes (cf. SAKAMURA 1920). Hence a transverse division of two non-homologous chromosomes, *e. g.* one of the long and one of the short chromosomes of *C. pilulifera,* must be two quite different things, requiring different forces and most probably not occurring at the same time. If chromosomes divide transversely, such divisions must, consequently, be supposed to take place in single chromosomes and not in whole sets simultaneously.

The investigations on the genetics and cytology of *Drosophila* (cf. MORGAN 1919, MOHR 1922, BRIDGES 1923) are of the greatest importance for our present question as for so many other problems. Some of the results of these investigations show that chromosomes really must be supposed to break transversely, the parts being united again in different ways. The phenomenon of crossing-over cannot be explained in any other way than by such transverse divisions of homologous chromosomes and rearrangement of the parts. This kind of transverse division must, moreover, be quite a regular phenomenon in many, or perhaps in all organisms. Much more interesting cases of transverse divisions of chromosomes in *Drosophila* are, however, the two phenomena »duplication» and »transposition», discovered by BRIDGES. In BRIDGES' case of duplication a piece must have been broken off from the middle part of one of the X-chromosomes in *D. melanogaster* and fastened to the end of the other X-chromosome, in his case of transposition (or translocation) a piece of one of the second chromosomes has been fastened to one of the third chromosomes.

Of special interest in this connection are the comparative, genetical

and cytological studies on different species of *Drosophila* carried out by several investigators (METZ 1918, STURTEVANT 1921 a and b, LANCEFIELD 1922, LANCEFIELD and METZ 1922). According to the results, as yet obtained, the X-chromosomes of *D. melanogaster, funebris, virilis* and *simulans* seem to be homologous, many of the mutant genes found being identical (or probably so) and their sequence in the chromosomes being the same. On the other hand, *D. Willistoni* and *obscura* have long V-shaped X-chromosomes (while the above-mentioned four species have rod-like X-chromosomes) and the genetical data indicate that the middle of these long X-chromosomes corresponds to one end of the X-chromosome in *D. melanogaster.* Hence the conclusion seems justified that the rod-like X-chromosome in the four first-mentioned species corresponds to one arm of the V-shaped X-chromosome in the two last-mentioned. Consequently the evolution of the different chromosome groups in the genus *Drosophila* has probably been connected with transverse divisions of chromosomes or fusions end-to-end in different ways. — An interesting case of such a fusion end-to-end of two X-chromosomes in non-disjunctional individuals of *Drosophila melanogaster* that possess either 3 X or 2 X + 1 y has recently been studied by LILIAN W. MORGAN (1922). These individuals behaved as if two X-chromosomes were united in meiosis, *i. e.* the normal criss-cross inheritance expected was not realized, but a non-criss-cross inheritance was found. The cytological investigation showed that two X-chromosomes had really fused end-to-end to a V-shaped chromosome that was sometimes very difficult to distinguish from the V-shaped autosomes. This fusion was perhaps only temporary but was nevertheless so strong as to change the results of the genetical experiments. — The *Drosophila*-investigations thus give strong evidence, both genetical and cytological, of the existence of transverse divisions and fusions end-to-end of chromosomes.

Reliable evidence of transverse divisions, obtained from direct microscopical observations, are to be found in the literature only in a few cases. The most significant observations are those, made by SEILER on certain *Lepidoptera.* SEILER and HANIEL (1921) investigated the chromosome cycle of *Lymantria monacha* and found the somatic chromosome number, counted in blastoderm-mitoses, to be 62, while the females have 31 and the males 28 in the heterotypic divisions. In the homotypic divisions both males and females have 28 chromosomes, so the mature eggs and sperma must also be supposed to have this number. In all metaphases with 28 chromosomes

there is one very long chromosome, much longer than any of the others, but in the 31-chromosome plates and in the somatic metaphases the long chromosome is replaced by 4 small ones. Excellent photomicrographs show the superiority of the microscopical slides. These remarkable observations show that four small chromosomes fuse to form a long chromosome which later splits up again into its four components. The fusion takes place before the reduction division in the males and in interkinesis in the females, the splitting up probably takes place at fertilization. As the compound chromosome is a long one and the part-chromosomes are short and as the splitting and fusion takes place in both the chromosomes of a geminus, we must conclude that the splitting is a kind of transverse division and that the fusion takes place end to end. The authors regard *Lymantria monacha* as a species in transition from one chromosome number to another, but they find it impossible, as yet, to decide in which direction the evolution goes. Moreover, they make comparisons between the cytological phenomena in *Lymantria* and the crossing-over in *Drosophila* and believe that both are only two sides of the same thing.

In another paper SEILER (1922) makes similar and very important observations on the cytology of *Solenobia pineti*. Of this species there exist individuals with different chromosome numbers, *viz.* 30, 31 or 32 (haploid). Each individual produces, as a rule, only one kind of eggs or one kind of sperma, but a mating of one female with one male gives very often larvae with different somatic chromosome numbers (61, 62 and 63 were found). This should most certainly be explained in much the same way as in *Lymantria* or by assuming the existence of a trivalent chromosome that may split up into two or three independent chromosomes. There exist apparently different races with different chromosome numbers. The elementary chromosomes may fuse again in the reduction division of hybrids between these races. Thus, for inst., a hybrid between the 30- and the 31-chromosome race may show in the heterotypic division either 30 or 31 chromosomes. SEILER says (p. 187): »1. In dem untersuchten Material von *pineti* befanden sich drei Chromosomenrassen mit haploid 30, 31 oder 32 Chromosomen und deren Kreuzungsprodukte. 2. Die Rasse mit 30 Chromosomen hat ein dreiwertiges Element, das in zwei oder drei selbständige Chromosomen aufsplittern kann. So entstehen die Rassen mit 31 oder 32 Chromosomen. — — — 4. In den Chromosomenbastarden wird scheinbar nur eine Sorte von Gameten gebildet. 5. Die verschiedenen Chromosomenzahlen innerhalb ein und desselben Geleges unmittelbar

nach der Befruchtung beweisen, dass tatsächlich doch ein Aufspalten stattfindet, und zwar sehr wahrscheinlich in die Gameten, aus denen ein Chromosomenbastard entstanden ist.» This species is also regarded as being in transition from one chromosome number to another, though there is no parallel changes in the exterior of the animals to be seen.

In a very thorough study on the numbers and dimensions of the somatic chromosomes in *Oenothera scintillans* HANCE (1918) states that in the somatic cells of this species the chromosomes vary in number from 15 to 21. In every plant cells with several of these numbers are found, though 15 is the most common number (»type number»), occurring in 45 % of all cells investigated. The additional chromosomes above the type number are believed, for the following reasons, to be produced through transverse fragmentation of the type chromosomes: a. Chromosomes are found in stages of constriction, indicating points at which fragmenting may take place. b. The sum of the lengths of the chromosomes is the same, whether the number be 15, 21 or any number between. c. The chromosomes can be arranged in pairs of equal length, distinct length-differences being found between the pairs. The differences between adjacent pairs in those cells that possess more than 15 chromosomes are not constant, as they are in the cells with the type number, which indicates that the length relations have been disturbed. d. By means of a special method the shortest chromosomes, regarded as fragments, can be joined with certain of the other ones and, when the chromosomes are now rearranged according to the new lengths, it is found that the pairing is much more obvious and that the new length relations of the pairs are practically identical with those, existing in the type cells.

HANCE believes that these four points prove conclusively that fragmentation of the chromosomes takes place in *Oenothera scintillans*. The present writer is of the same opinion and wishes, moreover, to point out that fragmentations must be normal processes in the cells, and not fixation artefacts. This is shown by the facts that they recur in the same proportion in subsequent years, that they seem to take place in definite chromosomes (the longer ones) and that they are found in anaphase plates, too, the latter fact being especially difficult to explain as an artefact which would most probably not occur in two anaphase plates simultaneously. — In addition, it should be mentioned that no fragmentation could as yet be found in the cells of the germinal line. This latter fact makes it possible that the frag-

mentation might have been incomplete, the fragments perhaps being joined with fine invisible threads. Anyhow, this fragmentation is of no influence on the germinal qualities of the race.

Miss LUTZ (1916) found *Oenothera*-mutants with a diminutive extra chromosome that may have arisen through fragmentation in much the same way as in *O. scintillans*.

In *Zea Mays,* studied by KUWADA (1919), certain phenomena occur that may be interpreted as transverse division of chromosomes, though the present writer is unable to regard KUWADA'S data, nor his illustrations, as quite convincing. The most significant facts are the following: Some individuals have 10 gemini of which 2 big ones, others 11 or 12 gemini of which 1 big resp. none. These relations seem to indicate that the 11th and 12th geminus may have arisen through fragmentation of one or two big gemini. As result of a cross between a race with 10 and another with 12 gemini individuals appear with but 10 gemini. This indicates that the big chromosomes in the 10-race conjugate with two (corresponding) small chromosomes each of the 12-race. One individual with 22 chromosomes in the root-tips had only 10 gemini in the pollen mother-cells, indicating a similar pairing.

Finally it should be mentioned that according to repeated observations the long chromosomes in the germinal cells of *Ascaris megalocephala* probably are composed of many small unit-chromosomes which separate from one another in the somatic cells. Similar fragmentations of chromosomes are known from several other investigations in animal cytology (*e. g.* HANCE 1917).

The investigations reviewed above show that most certainly transverse divisions of chromosomes occur, in animals as well as in plants, incidentally or, in some organisms, regularly. In chapt. 3 of the present work the conclusion was drawn, from measurements of the chromosome lengths, that the medium and small chromosomes in *C. pilulifera* and *C. panicea* probably have arisen through transverse division of long ones or, rather, that originally one long chromosome had divided into one medium and one short, a duplication of the three chromosome types having then taken place secondarily. In other words, the original chromosome set in the genus *Carex,* from which all the other sets should have arisen, probably was formed through an act of chromosome fragmentation. In the light of the above investigations this conclusion seems well justified.

It is interesting to note that exactly the same length relations between long, medium and short chromosomes were found by DE MOL

(1921) in *Hyacinthus orientalis,* and that this author drew the same conclusion as has been drawn in the present work. In *H. orientalis* the sum of the length of a medium and a short chromosome is equal to the length of a long one. From this and from certain observations on the shape and division mechanics of the chromosomes, DE MOL concluded that a medium and a short chromosome probably have arisen through transverse division of a long one.

In our discussion of the rôle of transverse fragmentations in the evolution of the chromosome groups in *Carex* we have thus arrived at the conclusion that such fragmentation has probably taken place at the formation of the fundamental set of this genus. Whether it has occurred later, too, contributing to the formation of the higher chromosome numbers in the genus is very difficult to decide.

The results, arrived at in chapt. 3, indicate that the same three types of chromosomes (long, medium and short) that are found in species with low numbers reappear in several of the species with high numbers. It is, however, somewhat uncertain, if all chromosome sets in *Carex* are composed of *only* these three chromosome classes. It seems, on the contrary, rather probable that some of the smallest chromosomes in the higher sets, *e. g.* the smallest chromosome in *C. rigida,* might be of secondary origin, *viz.* have arisen through transverse fragmentation of some of the longer ones. It is, of course, almost impossible to decide this question with certainty, especially because we have to deal with so high chromosome numbers, but the probability is there, nevertheless, and should not be overlooked. It must also be pointed out in this connection that the homology between the small chromosomes in *C. panicea* and those in *C. ericetorum* and *C. pilulifera* was found to be somewhat uncertain, indicating the possible existence of additional types of chromosomes and the possibility of rearrangements of the chromatic material connected with transverse divisions (cf. the differences between the X-chromosomes of different *Drosophila*-species, p. 175).

Finally a few lines should be devoted to constrictions of the chromosomes that seem to indicate the possibility of transverse fragmentations. In the heterotypic metaphases of many *Carex*-species such a constriction, in the middle of the gemini, is very often found, sometimes resulting in an almost complete transverse division. This constriction has been somewhat nearer studied in *C. sparsiflora.* It may occur in this species in both the big, the medium and the very smallest chromosomes, though it is generally found in but a few

of the latter ones, while it almost regularly occurs in the big gemini. The last-mentioned difference is probably due to the surface tension that makes the smaller chromosomes more resistant than the big ones to the forces that cause constriction. These forces seem to be something characteristic for the heterotypic divisions, as the constrictions can not be found in other stages, *e. g.* not in the homotypic metaphases. It is perhaps possible that the constriction offers an opportunity for transverse division, though this does not seem very probable. The extra chromosome, found in the aberrant plates of *C. montana* and *C. Goodenoughii* (textfig. 11), might perhaps be due to a fragmentation at the place, where the constriction regularly occurs, but, if this is really so, it seems uncertain, wheter these extra chromosomes would have maintained their individuality in the following stages, or if they would not rather have united again, their separation thus being incomplete and impermanent. Besides, they might as well be univalent chromosomes resulting from lacking conjugation. Though it might seem tempting to regard the transverse constriction of the chromosomes, so conspicuous in the heterotypic metaphases, as offering a possibility for transverse divisions, it seems, in fact, very uncertain, if these divisions ever become realized.

It is, besides, possible that the constriction might simply result from the homotypic division, beginning too early in some of the chromosomes. This explanation seems, however, not very likely, as the constriction, in fact, is a transverse one and does not occur with the same frequency in the different size-classes.

Although we must, consequently, count with the possibility of transverse divisions that might have given rise to new chromosomes, facts are, however, more favourable to the view that the higher numbers in this genus have arisen through duplication of entire chromosomes or, perhaps, that lower numbers might have arisen from higher ones through loss of chromosomes. It has already been shown that the same types of chromosomes reappear in different species, in species with many chromosomes as well as in those with few, and this speaks decidedly in favour of the view that a duplication (or perhaps loss) of entire chromosomes has taken place during the evolution of the genus. Another fact, speaking in favour of duplication, is the remarkable affinity between certain gemini, which are most probably homologous (perhaps identical), their homology of course being due to duplication. This affinity shows itself in the arrangement of the gemini in the heterotypic metaphases, where the gemini are grouped

in short rows (cf. p. 130) or in pairs. The arrangements in pairs is sometimes so close as to result in a kind of double gemini (cf. *C. glauca*, p. 160). — "The duplication (or loss) of chromosomes cannot have taken place in even multiples, as polyploidy does not occur in this genus. *It is, further, highly improbable that the duplication should have occurred in more than one or a few chromosomes at the same time* and this for the following reason.

It has been shown in chapt. 5 that nearly related species of *Carex* have chromosome numbers of about the same height, the difference in chromosome number between two species being, apparently, less, the more nearly related the species are. As it is probable that nearly related (or, rather, systematically very similar) species have a common origin or that some of them have given rise to the others, it follows that the evolution of a group of allied species or forms must have been connected with or, perhaps, caused by *small* changes in chromosome number. The evolution of allied species is of course the primary thing, more distantly related species arising secondarily through further genetical changes, often connected with new changes in chromosome number. It seems under these circumstances to the writer very unlikely that the evolution of the genus *Carex* should have been connected with any sudden great changes in chromosome number.

The only possible way by which such great changes might be explained would be to assume that the species should have arisen through crosses of the type described by FEDERLEY (1913) in *Pygaera*. In these bastards the conjugation of the chromosomes in meiosis is more or less lacking, the univalent chromosomes being arranged in the equatorial plane and there undergoing longitudinal division. The conjugation is somewhat varying in different cells. If *Carex*-hybrids behave in this way — which has not yet been possible to determine — the origin of a group of related forms with for inst. the haploid numbers 33, 34 and 35 might be explained in the following way: two species with $X = 17$ and 18 resp. cross, the F_1-generation thus getting the somatic number 35. If the conjugation of the chromosomes in F_1 entirely fails, the gametes receive 35 chromosomes and a new species with this haploid number may arise, if two chromosomes conjugate, the gametes receive 34 chromosomes, and if four chromosomes conjugate (into two pairs), the gametes receive 33 chromosomes, the new species now getting 34 and 33 respectively as haploid numbers. In this way the evolution of a new group of allied species with adjacent numbers might be connected with sudden, very great changes in chro-

mosome number. We must suppose, however, that the parent species of the new group survive, at least in some cases, and that the new species resemble these so much as to be referred to the same section in the system of the genus. Hence, in the above case, we must expect to get a systematic group of five species with the numbers 17, 18, 33, 34 and 35, but any such group with so different chromosome numbers has not yet been found in *Carex* and does, probably, not exist. The above scheme thus fails to explain the systematic distribution of the chromosome numbers in *Carex*.

Crosses according to the *Pygaera*-scheme probably occur in *Carex*. The present writer has not yet succeeded in analysing any *Carex*-hybrids, at least not any of known origin, but the general similarity of the meiotic figures in *Carex* and the *Lepidoptera* is, in fact, so striking that hybrids most probably must be supposed to behave in a similar way in both groups. The chromosome number and meiotic divisions of the presumed *Hornschuchiana*-hybrid, dealt with on p. 136, is quite in accord with this view. From what has been concluded above it is, however, obvious that such crosses cannot be supposed to have given rise to new species except, perhaps, in those cases, where nearly related species (with adjacent numbers) have crossed, giving rise to an F_1 with more or less complete conjugation and an F_2 with numbers, not much differing from the parent numbers. Moreover, the F_1-hybrids, analysed by FEDERLEY, as well as the *Carex*-hybrids, found in nature, are to a high degree sterile and, consequently, badly suited to give rise to new species.

We conclude: *the evolution of the chromosome numbers in Carex must have been a process of gradual changes, each number probably arising from the nearest lower (or perhaps higher) number.*

The essential part of this process has apparently been the origin of univalent chromosomes that have divided longitudinally in meiosis and thus given rise to gametes with extra chromosomes. These univalents have probably arisen through lacking conjugation. In chapt. 4 an aberrant heterotypic metaphase of *C. panicea* has been figured (textfig. 11) in which four A-chromosomes are seen, the fourth one apparently being the result of lacking conjugation in one of the gemini. Hence two of the A-chromosomes, seen in the plate, must be univalents but are, nevertheless, arranged in the same plane as the bivalents and probably divide longitudinally in the meiotic divisions. These divisions should give rise to a gamete with 17 chromosomes. The two pollen-prophases with four A-chromosomes, described in the

same chapter (textfig. 11), indicate that such gametes really are formed to a certain percent. The irregularities, found in *C. panicea,* are thus seen to agree with the above supposition of lacking conjugation. The few metaphases with one extra chromosome, found in other species (textfig. 11), show this chromosome in the equatorial plane, too. Though it is impossible to determine, whether the extra chromosome in these latter cases is a result of lacking conjugation or of transverse division, it must be supposed to give rise to an extra chromosome in the gametes, too, and is therefore not incompatible with the above views. Finally, it should once more be pointed out that the meiotic figures in *Carex* remind very much of the same stages in *Lepidoptera,* especially as far as concerns the remarkable accuracy with which the chromosomes arrange themselves in the equatorial plane. It seems, therefore, probable that univalents should behave in the same way in both groups, *viz.* divide in the meiotic divisions and become included in the gametes. Moreover, many plants, too, are known where univalents divide in the meiotic divisions (cf. TÄCKHOLM 1922, p. 261), though not always with the same accuracy. Facts thus tend to show that the above explanation of the origin of the extra chromosomes is the most probable one.

As to the cause of the failing conjugation very little can be said. It is possible that in some cases previous crosses might be responsible for the reduced affinity between the chromosomes thus exhibited. As, however, *Carex*-hybrids are more or less sterile, it seems unlikely that crosses could have played any greater rôle in this connection. Other eventual causes are unknown. — It may be remarked in this connection that the failing conjugation as a rule must have involved the small chromosomes, because of the fact that these obviously have multiplied more rapidly than the others and, consequently, now form a much greater part of the chromosome group in species with high numbers than in those with low numbers.

Another way through which gametes with differing chromosome numbers might have arisen is non-disjunction. In cases of non-disjunction both the chromosomes in a geminus go to the same pole in the heterotypic division. In that way four gametes arise of which two have an extra chromosome and the others a chromosome less than the normal gametes. Several instances of this phenomenon are known among both animals and plants, such as in *Drosophila melanogaster* (BRIDGES 1916, 1921), *Crepis Reuteriana* (ROSENBERG 1918), species of *Oenothera* (cf. GATES 1915, LEHMANN 1922) and *Datura*

stramonium (cf. BLAKESLEE 1921, 1923, BLAKESLEE, BELLING and FARNHAM 1923).

In *Crepis Reuteriana* which has 3 chromosomes (haploid; 1 long, 1 medium and 1 short) the conjugation between the two smallest chromosomes is often very loose, many pollen mother-cells containing two small univalents instead of one small geminus, and these univalents then often go to the same pole or one of them lags behind and gets lost in the plasma. Thus gametes with 2 and 4 chromosomes are produced in addition to normal ones. ROSENBERG believes that the lower chromosome numbers in *Crepis* (3, 4, 5) may have arisen through such irregularities in gametogenesis. It is seen that non-disjunction here is combined with imperfect conjugation which is also the case in *Oenothera,* according to GATES. In *Drosophila melanogaster* BRIDGES has found non-disjunction both in the sex-chromosome and in the small fourth chromosome. In *Datura stramonium,* finally, 25-chromosome mutants have arisen from diploid 24-chromosome plants, 49-chromosome mutants from tetraploid plants, as well as other, more complicated non-disjunctional mutants.

What does now happen to the aberrant gametes? As a rule they must be supposed to fuse in fertilization with normal ones, because they form but a small percent of the total number of gametes produced. Thus if a plant with $2\ X = 14$ sometimes produces gametes with 6 and 8 instead of 7 chromosomes, the offspring will contain a number of individuals with $2\ X = 13$ and 15, on rare occasions also individuals with $2\ X = 12$ and 16. In the meiosis of those plants that have the somatic numbers 13 and 15, 6 resp. 7 bivalents should be found and, in addition, 1 univalent. If this univalent chromosome does not now divide longitudinally in the meiotic divisions, it will lag behind, in a great number of cases at least, and become lost in the plasma. When such a process has been repeated for a few generations, only normal individuals with 14 somatic chromosomes and, perhaps, 12-chromosome individuals, too, will remain but no plants with odd numbers. That such an elimination of univalent chromosomes really takes place has been shown in the study of the offspring of *Oenothera lata* ($2\ X = 15$) and other similar 15-chromosome mutants of *O. Lamarckiana* ($2\ X = 14$), the offspring containing a *very* high percent of *Lamarckiana.* Similar results have recently been obtained by WINKLER and miss STOPPEL (1922) in breeding a triploid race of *Solanum nigrum.* It was found that the original triploid chromosome number of this race during several subsequent genera-

tions decreased, until the diploid number was reached, the decrease now halting. The eliminated chromosomes consequently were the univalent ones. It is thus clear that univalent chromosomes must divide longitudinally in meiosis, if they shall be kept in the following generations. In the above instance, the 13- and 15-chromosome plants would produce, if the univalents divide, gametes with 7 resp. 8 chromosomes only and, if selfed, they would give an offspring, consisting entirely of 14- resp. 16-chromosome plants. If the univalents divide in meiosis, non-disjunction consequently may give rise to a new race with the haploid chromosome number increased by 1 and the diploid number increased by 2. If, again, the univalents do not divide but — in a great many cells at least — lag behind and are lost, non-disjunction may give rise to a new race with 1 chromosome less in the haploid and 2 chromosomes less in the diploid phase and, in rare cases only, to additional plants with increased number.

If now two gametes with one extra chromosome unite, the two homologous extra chromosomes probably conjugate again in meiosis and the new race keeps its higher number as a constant character. This is an analogy to the $(2\ X + y + n) \times (2\ X + y)$ -type of bastards in *Hieracium* (ROSENBERG 1917). In that type some of the univalents (y) in the gametes that have fused and given rise to the bastard, had been homologous and, therefore, able to conjugate in meiosis.

For reasons, set about above, the writer is inclined to believe that univalent chromosomes in *Carex* really divide in meiosis. Hence it is probable that non-disjunctional processes, if they occur, should result in an increase in the chromosome number of the species. There is, however, as yet no direct evidence of non-disjunction, found in this genus, if not the fact that some species most probably lack the long A-chromosomes might be regarded as an indication of non-disjunctional processes. These chromosomes are found in the most primitive species investigated *(C. pilulifera),* and must therefore be supposed either to have gone lost or to have become fragmented transversely during the evolution of such species where they cannot be found *(e. g. C. ericetorum).*

As to our first explanation of the origin of gametes with differing chromosome numbers — that of lacking conjugation, accompanied by longitudinal division in meiosis of the univalents — it is clear that such a process, too, results in an increase in chromosome number. Other considerations lead to the same conclusion, *viz.* that *the evolution of*

the chromosome numbers in Carex probably has gone from low numbers to higher ones, or that the lowest numbers are the oldest and most primitive ones, while the highest numbers are the youngest. — The existence of several apparently homologous (or perhaps identical) chromosomes in the same haploid set *(e. g.* in *C. pilulifera* or in *C. glauca)* can hardly be explained in any other way than through duplication of chromosomes, a process that must have led to an increase in chromosome number. The reverse process, loss of chromosomes, would not explain this chromosome homology. — As appears from chapt. 8 the phylogenetic conclusions arrived at through taxonomical studies seem to agree best with the assumption that, in *Carex,* species and groups of species with high numbers are younger than those with low numbers. Thus the *Acutae* must be regarded as, very probably, a young group, and they have, in fact, some of the highest numbers hitherto found in the whole genus. — BRIDGES (1923) has pointed out that the loss of a chromosome in *Drosophila* produces much greater and more extreme changes than does the gain of that same chromosome. He also points out that in *Oenothera* as in *Datura* many mutants with $2n + 1$ chromosomes are known but not a single one with $2n - 1$ chromosomes. »These facts are interpreted to mean that the $2n - 1$ forms are such extreme departures from the type that they are unable to survive.» And more generally: »If minus deviations tend to cause more extreme and more lethal character changes than do plus deviations, then — — — the $n - 1$ gametes produced by non-disjunction should play a less direct rôle in evolution than do — — — the $n + 1$ gametes.» Hence the evolution must, as a rule, be supposed to have gone from low numbers to high ones (cf., however, the investigation on *Cyclops,* p. 163, the chromosome numbers of which are regarded as having been developed in the reverse direction). — Finally it is quite clear that in genera with *multiple* numbers the low numbers are more primitive than the high ones, as *no mechanism is conceivable through which a reduction in even multiples* (except halving, as in meiosis) *might have taken place (e. g.* from 45 to 36 in *Chrysanthemum).* It is then near at hand to regard — by way of analogizing — the low numbers in *Carex,* too, as primitive and the high ones as young. Otherwise *Carex* would present a rather peculiar exception, being perhaps the only plant genus in which the high chromosome numbers should be the primitive ones — an absurd result from a phylogenetic point of view.

As result of the considerations in this chapter the writer thus

arrives at the following opinions as to the evolution of the chromosome numbers in *Carex:*

1. Originally probably only long (A-) chromosomes existed in this phylum. By transverse division of a long chromosome a medium and a short one were produced. The original, fundamental chromosome group in *Carex,* from which all other groups have arisen, may thus, perhaps, have contained 3 (haploid) chromosomes, *viz.* 1 long, 1 medium and 1 short.

2. The evolution of the higher chromosome numbers from the

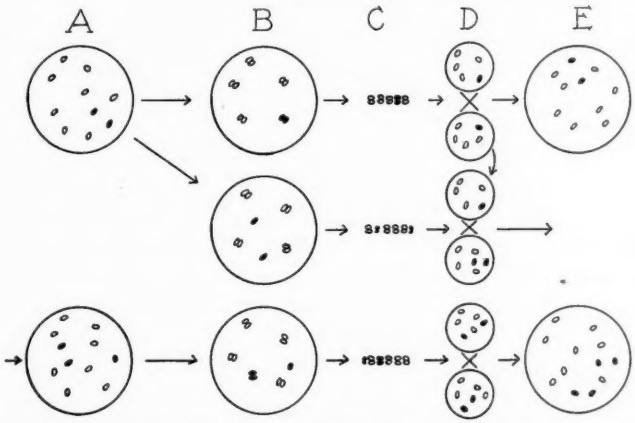

Fig. 12. Diagram of the evolution of a species with 2X=12 from a species with 2X=10. A somatic nuclei, B diakineses, C heterotypic metaphases, D fertilization, E fertilized egg-cells. — Upper row: complete conjugation, the old chromosome number kept. Middle row: conjugation failing in one pair of chromosomes, univalents being divided and an F_1-generation with 2X=11 arising. Lower row: self-fertilization of F_1, giving rise to an F_2 with 2X=12.

original one has been a process of small gradual changes, each number probably having arisen from the nearest lower number. No sudden great changes in chromosome number have taken place and, especially, no changes in even multiples, as there is no polyploidy to be found in this genus.

3. This gradual increase in chromosome number has been brought about through duplication of entire chromosomes (mostly small ones), in exceptional cases perhaps through transverse fragmentation of chromosomes.

4. The duplication has most probably been a result of failing conjugation between homologous chromosomes, the univalents, thus

produced, arranging themselves in the equatorial plane in the meiotic divisions and there being divided. In this way gametes with one extra chromosome have been produced. It is also possible that such gametes have been produced through non-disjunction. The aberrant gametes probable have fused with normal ones and, in the following generation, the extra, univalent chromosome must be supposed to have divided in meiosis, otherwise it most probably must have gone lost again in the meiotic divisions. Through fusion, in the third generation, of two such gametes with one extra chromosome each, a new constant race with the haploid number increased by 1 has been produced.

5. The cause of the lacking conjugation is unknown but might perhaps have been a result of previous crosses. It is, however, unlikely that crosses have plaid any greater rôle in the evolution of the chromosome groups in this genus, as *Carex*-hybrids are more or less sterile.

6. Facts tend to show that the evolution really has gone from lower numbers to higher ones, as has been indicated in the fore-going points.

A diagram representing the evolution, according to points 2—4, of a species with 12 chromosomes (2 X) from a species with 10 chromosomes, is given in textfig. 12.

VII. SPECIES-FORMATION IN THE GENUS CAREX.

From the conception of the evolution of the chromosome numbers in *Carex* developed in the preceding chapter certain conclusions may be drawn with regard to the species-formation in this genus. It was found that new chromosome numbers as a rule should have arisen through duplication of single chromosomes. In this way new forms should have arisen with two extra chromosomes in their somatic cells and, as a result of these extra chromosomes, certain new characters in their exterior. As pointed out in the fore-going chapter, the primary step has probably been a new form with one extra somatic chromosome, the definite new race with two extras having arisen in a subsequent generation. The first step in the formation of a new species has thus probably been a mutation of the *Oenothera lata*-type or of the type found in *Datura*. The second step has been a mutation, probably corresponding to the 16-chromosome mutants in *Oenothera* (LUTZ 1917). These »chromosome-mutations» in

Oenothera and *Datura* show differences from the parent type in several clear points, and the same must be supposed to be the case with the corresponding mutants in *Carex*. Further it should be pointed out that mutants with extra chromosomes seem to form the majority of the mutants in the genus *Oenothera* (LEHMANN 1922, p. 366, GATES 1923). Also in *Datura* such mutants are common, and hence it seems probable that they might have been of great importance for the evolution of the genus *Carex* as well.

Mutations, involving the loss of a chromosome, have perhaps occurred, too, though, for reasons set forth in the preceding chapter, they have probably been of inferior importance.

Other types of mutations are those that depend upon changes within a chromosome, either changes of single genes or of whole sections of the chromosomes, according to the conceptions of the *Drosophila*-investigators (cf. also the »Komplexmutationen» of NILSSON-EHLE 1920). Nothing is as yet known about the eventual existence of such mutations in *Carex,* but probably they occur in this genus as in several others and play a rôle in the formation of new species.

Transverse fragmentation of chromosomes — if such occur, and perhaps also end-to-end fusions — should result in new linkage relations between the genes and may thus be of importance in the recombination of the characters. The fragmentation must of course play the greater rôle, as it should cause *increased* combination possibilities and, consequently, increased variation of the species.

The rôle of hybridization in the evolution of new species in *Carex* shall now be briefly considered. Two alternatives must be distinguished. Either a cross between two different species or forms is accompanied by irregularities in the meiosis of the hybrid and changed chromosome numbers in the further generations, or the meiotic divisions are carried out regularly, and the chromosome number is maintained unchanged. The latter case requires of course as a supposition the same chromosome number in both parents. Now it appears from the considerations in the preceding chapter that crosses, accompanied by great changes in chromosome number, cannot have been of any importance in the processes of species-formation in *Carex*. Crosses, involving small changes, again, have probably contributed to the formation of new species, though, apparently, not in any higher degree. Crosses between forms so nearly related as to have equal chromosome number and giving hybrids with regular meiosis must have given rise to new forms through typically Mendelian segregations. It is thus seen

that hybridization within this genus must have acted in two different ways, through Mendelian segregations (regular meiosis) and through irregular chromosome distribution.

The writer is inclined to regard hybridization as a factor of somewhat inferior importance for the formation of new species in *Carex*. Hybrids with irregular meiosis probably arise through crosses between species or forms that are not so similar or closely related as to give a fertile offspring. Irregular meiotic divisions are very often accompanied by pollen sterility. Hence such hybrids should probably be sterile to a great extent. As pointed out in the previous chapter, *Carex*-hybrids, found in nature, are mostly sterile and consequently do not give rise to new species. As, on the other hand, nearly related species very often show different chromosome numbers, their origin must have been connected with something more than mere Mendelian segregation, *viz.* just a change in chromosome number. Hence crosses of the Mendelian type are, neither, sufficient to explain the species-formation in this genus. The best explanation seems to be that of mutations of the *lata*-type as set about above. It should, moreover, be pointed out that nearly related species exist with the same number of chromosomes, but whose chromosome groups nevertheless contain different components. Table 5 (p. 157) shows that *C. sparsiflora* and *C. panicea* have different chromosome groups, though both species have 16 chromosomes. This means that, from the fact that two related species have the same chromosome number, it is not allowed to conclude that these species have arisen through mere Mendelian segregations or through mutations within the chromosomes, without further changes in the chromosome set.

It is of course difficult to estimate the relative importance of the different processes that have co-operated in the formation of new species in *Carex*. The writer regards the »chromosome-mutations» that have given rise to new chromosome numbers and, in connection with them, mutations, caused by changes within the chromosomes, as the most important processes in the evolution of new species. New factors, arising through mutation, have of course later segregated according to the Mendelian scheme. Hybridization is regarded by the present writer as of somewhat inferior value. The writer wishes especially to emphasize that the occurrence of so many different chromosome numbers in *Carex* makes it quite impossible to explain the species-formation in this genus as a mere result of Mendelian segregations. Thus the views on evolution set forth by LOTSY (1916) or

HERIBERT-NILSSON (1918), are inadequate and do not explain more than certain parts of the evolution (cf. chapt. 9).

VIII. PHYLOGENY OF THE GENUS CAREX. AGE AND AREA.

In chapt. 5 it was found that *Carex*-species, belonging to the same section of the genus, have chromosome numbers of about the same height, groups of adjacent numbers thus being obtained, when the species are arranged according to systematic relationship. Further it was suggested that the chromosome numbers of a group of related species may be estimated, approximately, when the number of one species of the group is known. In chapt. 6, again, it was stated that most probably the evolution of the chromosome numbers in *Carex* has gone from low numbers to higher ones. Species and groups of species with low numbers should thus be more primitive than those with high numbers. These results must be of great importance in all attempts to trace the phylogeny of the genus *Carex* and its different subgenera and sections. If due regard is paid to the above results all phylogenetic lines must be drawn from groups with low numbers to those with higher ones and, moreover, if a group of species, from other reasons, is supposed to have descended from another group but the former is found to have lower numbers than the latter, this descent must be rejected as impossible. It is of course necessary to draw such conclusions with great care in cases, where only one or two numbers are known in each of the groups under consideration and the numbers known do not differ much from one another. On the whole, however, the chromosome numbers must be of great value in phylogenetic studies on *Carex*.

The largest subgenus of *Carex* is *Eucarex* of which KÜKENTHAL'S monograph (1909) contains 533 (»good») species out of 793 or more than half of the whole genus. It is also the subgenus of which the present writer has investigated the greatest number of species. Hence we will begin our phylogenetic considerations with this subgenus.

The lowest numbers, hitherto found in *Eucarex* (and in the whole genus), are those in the groups *Montanae* and *Paniceae*. These sections should thus belong to the most primitive ones. The section *Montanae* is circumscribed in a somewhat different way by different authors. According to ASCHERSON and GRAEBNER in their Synopsis (1902—04) both *C. caryophyllea* and *C. tomentosa* are referred to this

section in addition to *C. ericetorum, montana, pilulifera* and several species not investigated by the present writer. HOLM (1903) also places the above-mentioned five species together, as do several works on the Swedish flora. KÜKENTHAL, again, in his great work separates them and refers the three last-mentioned to *Montanae* but places *C. caryophyllea* among the *Mitratae* and *C. tomentosa* among the *Pachystylae*. The chromosome numbers of these species show that KÜKENTHAL undoubtedly is right in separating them. The numbers are 9, 15, 19, 24 and 31, thus ranging over a much greater field than in any other section investigated. The chromosome numbers of the three species, referred to *Montanae* by KÜKENTHAL, agree rather well, though *C. pilulifera* seems to deviate somewhat, especially as the differences in chromosome size are greater in this species than in the others. — Sect. *Montanae* is thus one of the most primitive groups, hitherto investigated, as is the case, too, with sect. *Paniceae*. *C. pilulifera* is the most primitive species of all investigated by the writer.

Another rather primitive group is sect. *Digitatae* with two chromosome numbers determined, *viz.* ca. 23 and 26. Other groups, placed by KÜKENTHAL in the neighbourhood of *Montanae, Paniceae* and *Digitatae* and probably more or less related to them, are *Pachystylae, Lamprochlaenae, Mitratae, Albae, Limosae* and *Griseae*. It seems probable that also these sections represent somewhat primitive conditions, though but few chromosome numbers have as yet been determined. It is seen that those sections in *Eucarex* which thus should be primitive contain species of low stature with only one male spike, 3 stigmata and utriculi generally without or with but a short rostrum that is generally not bidentate. It appears, too, that most of these apparently primitive species prefer dry soil and grow on rocks, grass-ground or in forests.

From these primitive groups several phylogenetic lines might be traced with the aid of comparative morphological studies and a confirmation of the supposed relationship be sought in the chromosome numbers.

One such line probably leads over the *Atratae* to *Acutae*, though it is impossible to decide exactly from which primitive group the *Atratae* should have descended. That *Atratae* and *Acutae* are related to one another has been suggested by several authors. Thus ALMQUIST (1884) expresses the opinion that the *Acutae* have descended from the *Atratae* and, besides, that all distigmatic *Carices* have descended from tristigmatic ones. HOLM (1903) places the two groups together (though

under other names) and the *Atratae* first, indicating that this group should be the more primitive one. BAILEY (1886), ASCHERSON and GRAEBNER (1902—04) and KÜKENTHAL (1909) place them also together, but KÜKENTHAL (1900) expresses the singular view that tristigmatic *Carices* have descended from distigmatic ones and that the *Atratae* thus have descended from the *Acutae*. The above authors thus all agree in regarding the two groups as nearly related but have different opinions as to which of them is the more primitive one. The chromosome numbers in the present work show that the *Atratae* undoubtedly should be regarded as more primitive and have given rise to the *Acutae,* as suggested by ALMQUIST. On the whole it seems extremely probable that all distigmatic species have descended from tristigmatic ones, as three carpels characterize the typical monocotyledonous flower.

As to the phylogeny of the different subsections within *Acutae*, the *Rigidae* seem to be more primitive than the *Vulgares* and *Caespitosae,* which agrees well with the classification adopted by KÜKENTHAL. The view, expressed in BAILEY'S classification as well as in the Swedish flora by KROK and ALMQUIST, that *C. rigida* should be a variety or a subspecies of *C. Goodenoughii* is certainly erroneous.

A special interest deserves *C. glauca* MURR. (= *flacca* SCHREB.). ASCHERSON and GRAEBNER (1902—04) place it together with *C. trinervis* DEGL., *C. hispida* WILLD., *C. panicea* L. and *C. vaginata* TAUSCH. and they say in the introduction to the *Heterostachyae* that *C. glauca* is nearly related both to the *Acutae* (through the distigmatic *C. trinervis*) and to *C. panicea* and *C. vaginata.* KÜKENTHAL (1909), again, separates *C. glauca* from the two last-mentioned species and places it together with *C. hispida* and some other species in sect. *Trachychlaenae.* HOLM (1903) places it in the same section. Referring to the great difference in chromosome number between *C. panicea* and *vaginata* (= *sparsiflora*) on the one hand (X = 16) and *C. glauca* on the other (X = 38), the present writer cannot regard these species as nearly related. Hence it seems quite right to separate them, but there is, nevertheless, a conspicuous similarity between *C. glauca* and the two other species to be found in the chromosome sets, *viz.* as regards the size differences between the chromosomes. The difference in size between the biggest and the smallest chromosomes is quite as great in *C. glauca* as in *C. panicea* and so great a difference has, moreover, not yet been found in any other species except in *C. pilulifera.* This seems to indicate that *C. glauca* should be related to *C. panicea*

though not very nearly. The writer finds it very probable that a phylogenetic line may be drawn from sect. *Paniceae* to sect. *Trachychlaenae*. If any phylogenetic relations exist between *Trachychlaenae* and the *Acutae,* on the other hand, seems more uncertain, but perhaps a line might be drawn from the primitive *Paniceae* via *Trachychlaenae* to the *Atratae—Acutae*. It should be noted in this connection that rather great size-differences have been found in *C. atrata, rigida, aquatilis* and *Hudsonii,* too (cf. p. 157), whereas more conspicuous differences in chromosome size not yet have been found in species, belonging to other groups, except in sect. *Montanae*. It seems thus, as if a phylogenetic line, characterized, *inter alia,* by great differences in chromosome size, might be drawn as follows: *Paniceae* → *Trachychlaenae* → *Atratae* → *Acutae* (these groups taken according to KÜKENTHAL 1909). The last of these groups, which is the youngest, is the greatest and most critical one, and its adaptation to wet localities is more developed than the others.

An, apparently, very natural phylum is represented by the sections *Pseudo-cypereae, Physocarpae, Paludosae* and *Hirtae*. The species, belonging to these sections, are generally large and coarse, most of them have more than one male spike, almost all have three stigmata. The utriculi have a long rostrum that is conspicuously bidentate. The leaves have strong transverse nerves that give them a reticulate surface. The paludose habit is decidedly developed. These groups have high chromosome numbers and should thus represent young and specialized types. The chromosome numbers indicate that an evolutional line probably has gone from *Physocarpae Lupulinae* to *Ph. Vesicariae,* that *Pseudo-cypereae* does not belong to the very youngest and most developed groups and that of *Paludosae* and *Hirtae* — nearly related according to several of the authors, cited above — the former is the more primitive group. *C. hirta* (X = 56) is by far the most developed species, hitherto investigated by the writer. These four groups are the result of an evolution, through which species of a characteristic habitus and a rather uniform biological type have been developed. The climax of this evolution is represented by sect. *Hirtae*.

It is somewhat difficult to connect this phylum with the primitive groups of the subgenus. An intermediate position is held by *Spirostachyae* (X = 28—37) which perhaps might be connected with the *Secalinae* and the *Physocarpae Lupulinae,* as well as with *C. pallescens* (X = 32). The latter species is placed among the *Pachystylae* by KÜKENTHAL and accordingly regarded as in some degree related to

the primitive *Montanae,* together with the primitive species *C. panicea* and *C. vaginata* by HOLM and in the neighbourhood of these species by ASCHERSON and GRAEBNER but together with the *Spirostachyae* by BAILEY. The present writer is inclined to regard KÜKENTHAL'S classification as the best but finds it probable that this species may be related to the *Spirostachyae,* too. It is thus possible that the phylum, considered above, might be traced back via *Spirostachyae* to the neighbourhood of *Montanae.*

The material, brought together in the present work, does not permit of any further speculations as to the phylogenetic relationships of the different sections within the subgenus *Eucarex.* As concluding remarks we state that the evolution has gone from small to large and coarse species and from dry soil into swamps and bogs. The order by which KÜKENTHAL has arranged the sections of *Eucarex* is apparently a fairly good expression of their phylogenetic relationships, but the evolution has begun in the *middle* of KÜKENTHAL'S system and has proceeded to both ends, probably also deviating into smaller ramifications. It is interesting to note that KÜKENTHAL'S system begins with *Acutae* and ends with *Hirtae,* these groups containing the highest chromosome numbers, hitherto found by the present writer.

The subgenus *Vignea* is much more homogeneous than *Eucarex.* Thus KÜKENTHAL (1900) says that *Vignea* seems to be a more firmly established subgenus than *Eucarex.* It has two stigmata throughout, contains much fewer species (139 according to KÜKENTHAL 1909) than *Eucarex* and is much less variable than the latter subgenus. In *Eucarex* there are many great variable groups of species but relatively few in *Vignea.* Hence the latter subgenus certainly must be regarded as more homogeneous and uniform than the former. KÜKENTHAL'S conclusion that *Vignea* is an older subgenus than *Eucarex* seems, however, not to be quite correct, as the latter subgenus contains both older and younger groups than the former, judging from our present knowledge of the chromosome numbers.

The conclusion that *Vignea* is a more uniform subgenus than *Eucarex* is confirmed by the chromosome numbers hitherto determined. Of the 29 sections of *Eucarex,* distinguished by KÜKENTHAL (1909), the present writer has as yet investigated 14, finding in these sections chromosome numbers ranging from 9 to 56. Of the 20 sections of *Vignea,* again, 7 have been investigated, showing chromosome numbers, ranging only from 27 to 34. It seems thus clear that *Vignea* is a very homogeneous group of an average age. Any

reliable conclusions as to the phylogenetic relations between the sections within *Vignea* can not, of course, be drawn from so little variable chromosome numbers.

As to the monostachyous species (60 species according to KÜKENTHAL 1909) of *Carex,* they have generally been thrown together into a special subgenus *Monostachyae,* or *Primocarex,* as it is called by KÜKENTHAL (1909). With the latter name KÜKENTHAL wishes to express that this should be the most primitive subgenus in *Carex.* Other authors, again, maintain that the monostachyous species are of polyphyletic origin and that they, consequently, should be distributed among the groups of the other subgenera (cf. BAILEY 1886, HOLM 1903). ASCHERSON and GRAEBNER, too, regard the subgenus *Monostachyae* (= *Psyllophorae*) as being of polyphyletic origin, though they retain the name for practical purposes.

On account of the difficulty to obtain fixed material of the monostachyous species, the writer has not yet been able to determine the chromosome numbers of more than two of these species, *C. dioica* (X = 26) and *C. rupestris* (X = 25). These two species can, on account of their numbers, not be regarded as very primitive. *C. dioica* is, moreover, regarded by several authors as nearly related to certain homostachyous species, especially to *C. stellulata* GOOD. and its allies. The chromosome number of *C. stellulata* is unknown, but the related *C. elongata* has about 28 chromosomes. Hence it seems probable that the sections *Dioicae* and *Elongatae* really are related to one another. In the same way *C. rupestris* is regarded as related to *C. pedata* WAHL. The chromosome number of the last-mentioned species is unknown, but KÜKENTHAL places it among the *Eu-digitatae* of which two other species have been investigated by the present writer, *viz. C. digitata* (X = 26) and *C. ornithopoda* (X = ca. 23). Thus the affinity between *C. rupestris* and *C. pedata* as well as the whole *Digitatae* seems probable. Other authors, however, place *C. pedata* among the *Lamprochlaenae* of which no chromosome numbers have as yet been determined.

The chromosome numbers thus show that *Dioicae* and *Petraeae* cannot be any very primitive groups, but that they may very well be related to *Elongatae* and *Digitatae* resp. It is also suggested by several authors (BAILEY, HOLM, ALMQUIST) that *C. scirpoidea* MICHX is nearly related to *Montanae,* especially to *C. ericetorum.* As the *Montanae* are primitive, the same might be supposed to be the case with *C. scirpoidea.* It seems thus, as if the monostachyous species

should be of different age, some being primitive and others somewhat higher developed. They are connected in different ways with the other subgenera but might nevertheless be regarded as ramifications of a

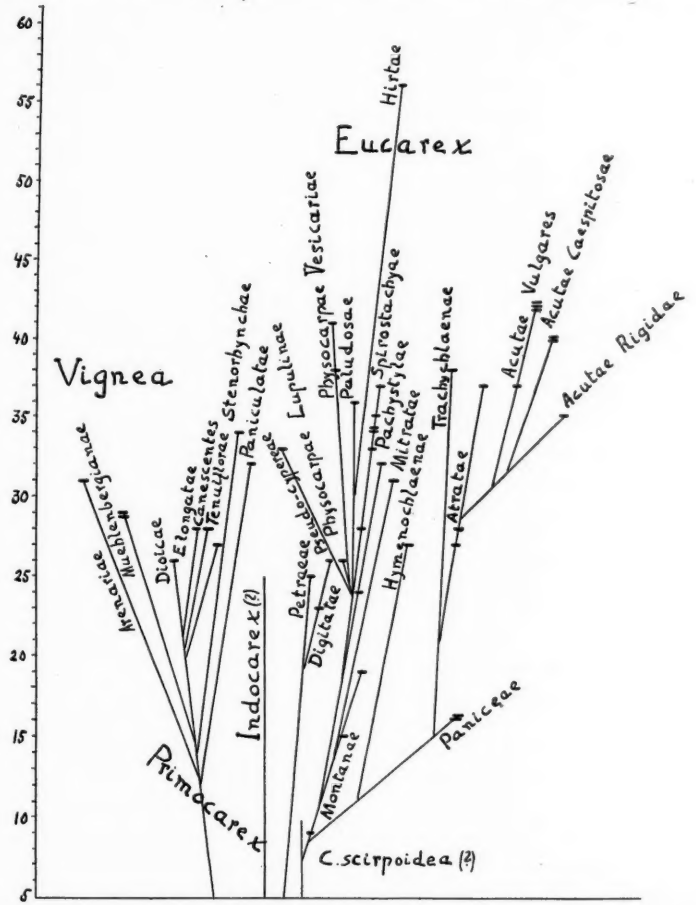

Fig. 13. Phylogeny of the genus *Carex*, considered in relation to the chromosome numbers (given in the scale to the left). The horizontal solid lines represent the species and forms in table 1.

common stock. The present writer agrees with KÜKENTHAL that the monostachyous species should be kept together as a special subgenus which probably should be regarded as, on the whole, more primitive

than the others and thus deserving the name *Primocarex*. Of this subgenus, however, only isolated groups now survive, representing ramifications, many of which do not now stand in any closer relation to one another but are nearer related to different groups of *Vignea* and *Eucarex*. From this view it follows that *Eucarex* perhaps might be to some extent of polyphyletic origin. Thus *Digitatae* might be supposed to have descended from *Petraeae*, whereas *Montanae* should have descended from *C. scirpoidea* or some allied species, now extinct. *Montanae* is certainly related to several of the younger groups of *Eucarex* what does not, however, seem to be the case with *Digitatae*, the latter probably being a side-line of less phylogenetic importance. Finally we state that *Elongatae* probably has descended from *Dioicae* and, as *Vignea* on the whole seems to be a rather homogeneous subgenus, it might be suggested that many of the sections of *Vignea* may have had a similar origin.

In the fourth subgenus, *Indocarex* (61 species according to KÜKENTHAL 1909), the writer does not know a single chromosome number; it is therefore difficult to draw any phylogenetic conclusions. One thing seems, however, quite clear: KÜKENTHAL'S view that *Eucarex* has descended from *Indocarex* cannot be right, as the primitive *Eucarices* show very little similarity with the different types of *Indocarex*. Probably *Indocarex* and *Eucarex* represent parallel lines.

A diagram of the phylogenetic views, developed above, is given in fig. 13. It should be pointed out that these views probably must be modified, when more chromosome numbers become known.

AGE AND AREA.

According to the Age and Area hypothesis, set forth by WILLIS (cf. WILLIS 1922), the area of distribution of species, genera and higher groups of plants is, on an average, a function of the age of the species and groups. On an average, the endemics of a country must be younger than the wides and, on the whole, the smaller areas, species or genera occupy, the younger they are, and the wider their distribution, the higher their age. It is expressly emphasized by WILLIS that the law of Age and Area holds good only for averages of a number of species and not for single species as, in dealing with averages, many casualties are excluded. On p. 63 of the above-mentioned work WILLIS gives the following expression of the rule of Age and Area: »The area occupied (determined by the most outlying stations) at any given time, in any given country, by any group of allied species at least

ten in number, depends chiefly, so long as conditions remain reasonably constant, upon the ages of the species of that group in that country, but may be enormously modified by the presence of barriers such as seas, rivers, mountains, changes of climate from one region to the next, or other ecological boundaries, and the like, also by the action of man, and by other causes.»

The rule of Age and Area is chiefly founded on statistical studies on the endemics of Ceylon and New Zealand and seems to be fairly well founded as regards these island floras. How far it may be applied on the general questions of geographical distribution is difficult to decide. The object of the following lines is merely to show one way by which the validity of the hypothesis might be tested.

As appears in the next chapter, a good many plant genera are now known in which species with several different chromosome numbers are found. In most of these cases the numbers — or at least part of them — form multiples of a common fundamental number. As has already been pointed out (p. 186), the higher of these multiple numbers must have been derived from the lower ones and, consequently, it may be concluded that species with high (multiple) numbers are younger than those with low numbers. The studies on *Carex* in the present work have lead to a corresponding result, though the chromosome numbers in this genus do not form multiples. This gives us an exact method at hand by which the Age and Area hypothesis might be tested. *If the chromosome numbers of a group of allied species — endemics and wides — be determined, the endemics must be supposed to have, on an average, higher chromosome numbers than the wides.*

Unfortunately, the material brought together in the present work on *Carex* does not allow of any comparisons between endemic and wide-spread species. The writer has, however, tried to test the hypothesis in another way, by comparing the geographical distribution of some old and young *groups* of the genus. The results are not very conclusive but may be partly published, nevertheless, as this method of studying the Age and Area hypothesis is a new one.

It is clear and it has been set about by WILLIS that, if the rule of Age and Area holds good in comparing the distribution of allied *species,* it must hold good in comparing *groups* of species, too, or whole genera and families. In the present case the writer has made the following considerations. The »natural» groups, in which a genus is divided by systematists, are generally regarded as of monophyletic

origin. As a rule, the more natural they are, the more likely they are to be monophyletic, *i. e.* to have descended from one species as a common ancestor. This species must originally have been an endemic in the country where it arose. In spreading gradually, it gave rise to a number of new species, these new species later in their turn giving rise to still other species. In this way a group arose, containing nearly related species that necessarily must have been *grouped geographically round the place where the evolution originally began* (a similar argumentation is found in the above-cited work by WILLIS, p. 76). Later, when the group spread over larger areas and the formation of new species for some reason perhaps ceased or decreased, the country, where the group had had its origin, might no longer be detected. When the group arrives at its climax of evolution, it probably covers vast areas, and its species are probably rather uniformly distributed. Still later it may happen that members of the group are exterminated from certain parts of the world, where they formerly occurred, and a discontinuous distribution results. It thus appears that species of young groups should be found grouped round a centre, representing the place where the evolution of the group originally began, that species of older groups should be distributed over large areas without showing any grouping round the original centre and that, finally, very old groups should show discontinuous distributions.

From this point of view some of the sections of *Carex,* according to the classification of KÜKENTHAL (1909), have been laid down on maps, a few of which are published in fig. 14—22. The data on the distributions are taken from KÜKENTHAL'S book. As representatives of old groups *Montanae* and *Paniceae* are given. Young groups are *Acutae, Physocarpae Vesicariae* and *Hirtae.* Finally two special phylogenetic lines are illustrated, *viz.* the one running from *Atratae* to *Acutae* and that from *Physocarpae Lupulinae* to *Ph. Vesicariae.*

A glance at the maps shows immediately that clear differences between old and young groups are difficult to find. Young groups occur with very uniformly distributed species *(Hirtae, Vesicariae)* or conspicuous discontinuities *(Acutae Vulgares),* as well as old groups with certain centra of distribution *(Montanae).* The maps of *Atratae* and *Acutae Vulgares* show practically no difference at all. These two groups have a very similar distribution. Note especially the species on the southern hemisphere! On the other hand, *Acutae Vulgares* seems to have a more conspicuous centre (in pacific North America) than *Caespitosae* and *Rigidae* which are probably older. A compa-

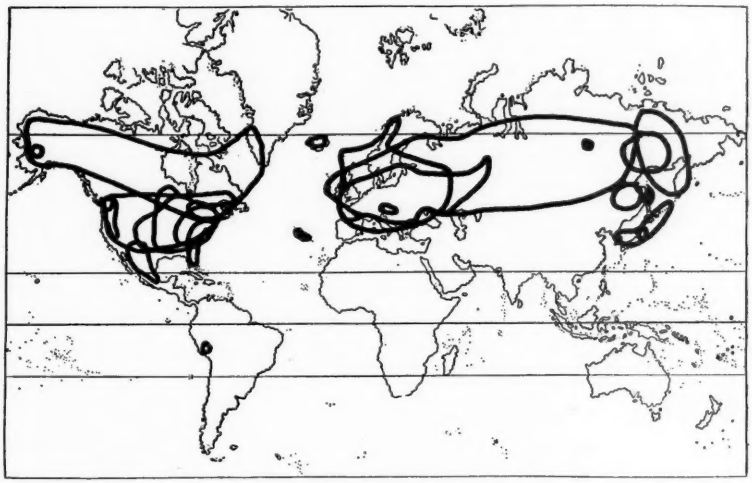

Fig. 14. *Montanae.* 18 species.

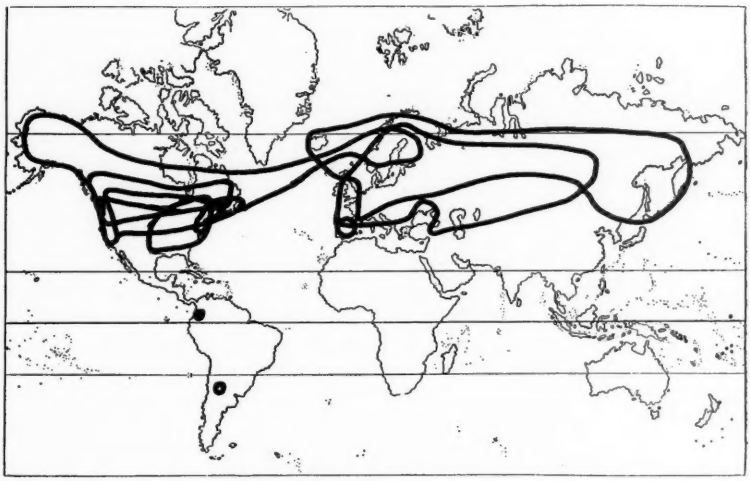

Fig. 15. *Paniceae.* 9 species.

rison between *Physocarpae Lupulinae* and *Vesicariae* shows further that the former group should be older, as it shows a very discontinuous distribution, while the latter is rather uniformly distributed over a vast area. It should be pointed out that *Lupulinae* contains species

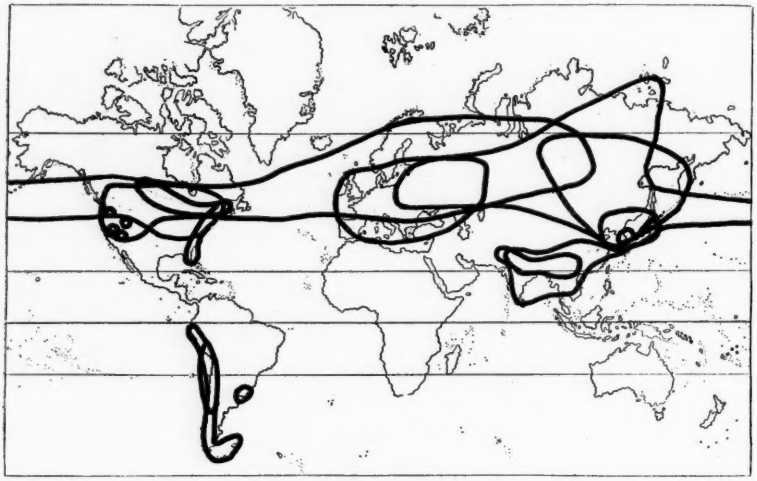

Fig. 16. *Hirtae.* 16 species.

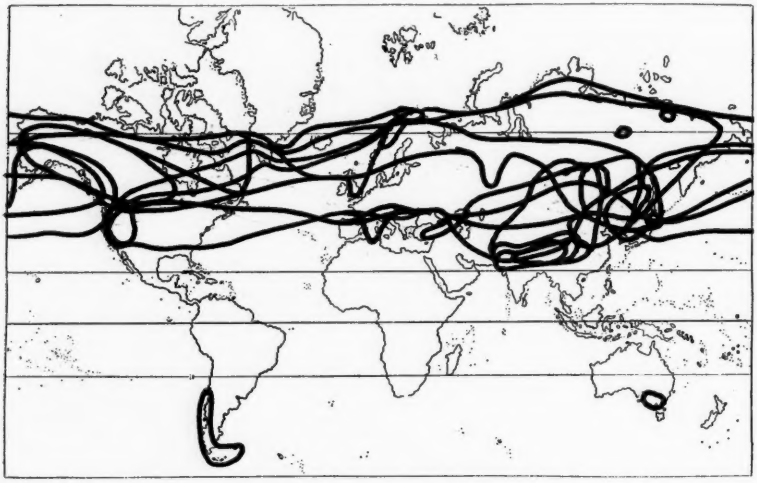

Fig. 17. *Atratae.* 21 species.

of a very conspicuous and characteristic appearence. Hence it is improbable that these species should have been overlooked to any greater extent: the map probably gives a fairly good idea of the real distribution of the group. It should further be noted that *C. Michaux-*

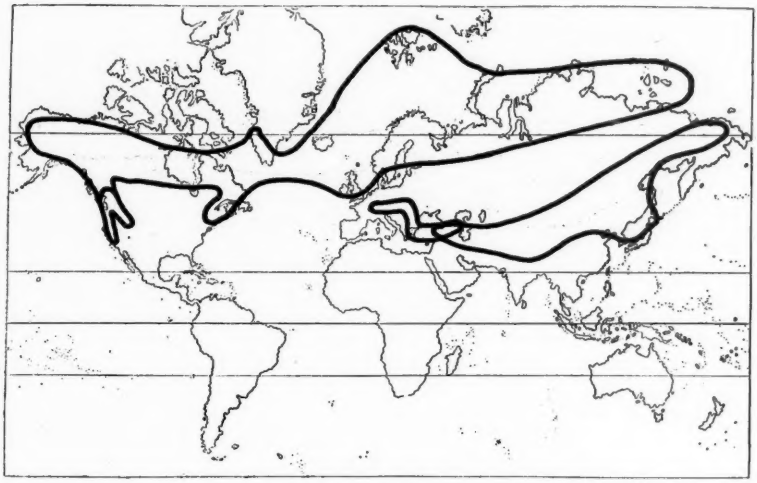

Fig. 18. *Acutae Rigidae.* 3 species.

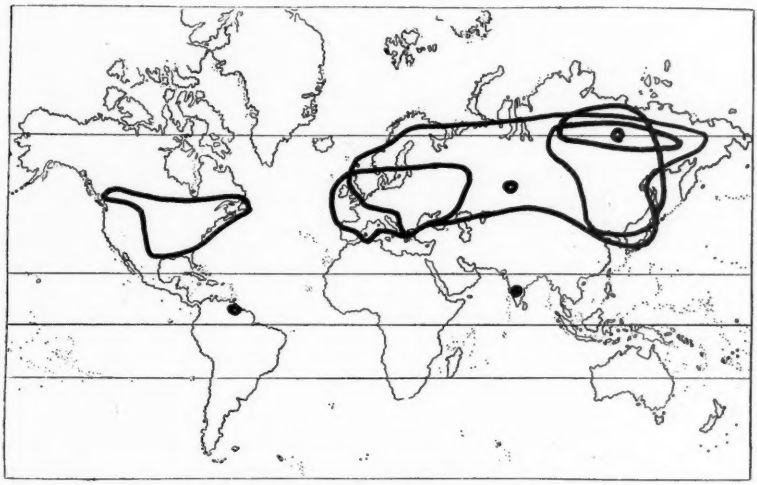

Fig. 19. *Acutae Caespitosae.* 9 species.

iana has been found both in boreal-atlantic North America and in Kamtschatka and Japan. *Lupulinae* is thus a group of very discontinuous distribution, but it appears, on the other hand, that in atlantic North America an evolution of new species within the group has taken

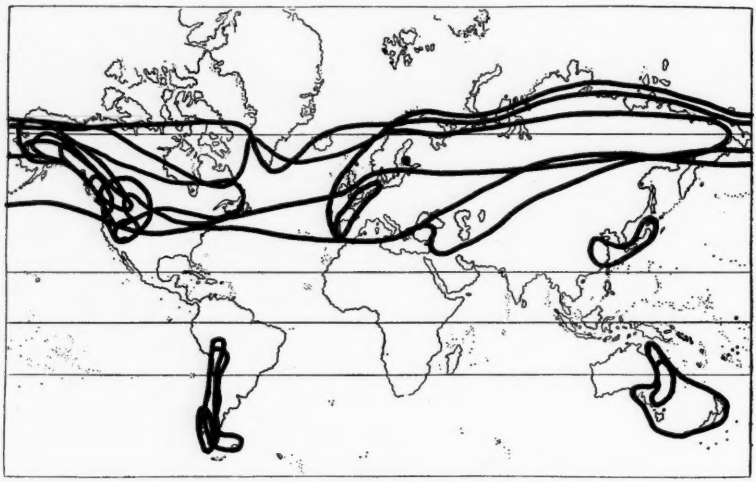

Fig. 20. *Acutae Vulgares.* 14 species.

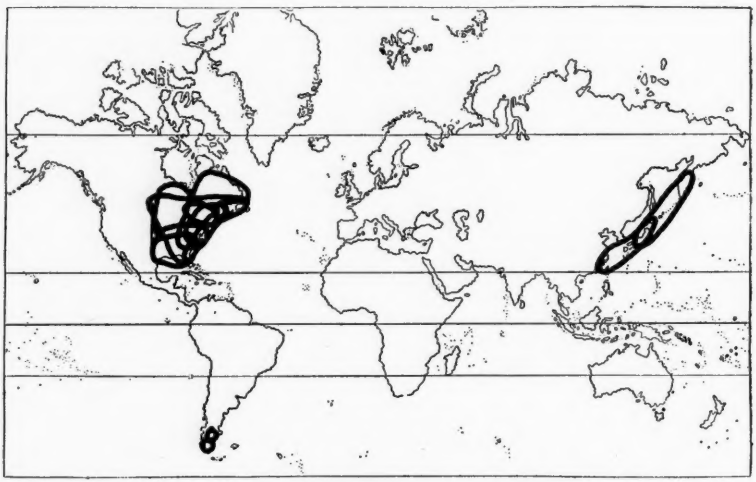

Fig. 21. *Physocarpae Lupulinae.* 11 species.

place secondarily. Such secondary centra of species-formation must necessarily render investigations of this kind still more difficult. The relations between age and area seem on the whole to be rather complicated and all conclusions should be drawn with great care. Clear

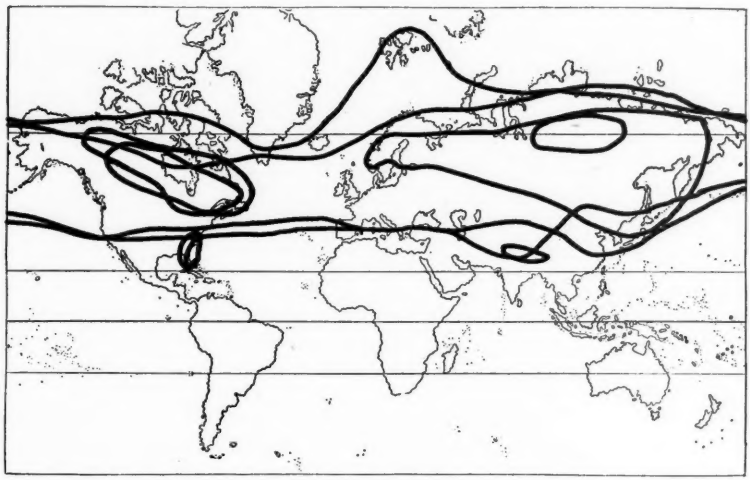

Fig. 22. *Physocarpae Vesicariae.* 9 species.

results can probably be obtained only from comparisons between nearly related *species,* belonging to the same section of the genus, particularly if they belong to the same country. From the maps in the present work apparently only one thing appears as somewhat certain: all the groups, laid down in the maps, even the youngest of them, are probably *very old,* perhaps from the tertiary period. — The genus as such is known from Eocen.

IX. COMPARISONS WITH OTHER GENERA. DIFFERENT PROCESSES OF SPECIES-FORMATION.

Chromosome numbers are now known from a considerable number of plant genera. In the following an attempt is made to classify some of the best-known of these genera from the point of view of their chromosome numbers. The data are found in the compilation, made by TISCHLER (1921—1922, p. 552—588 and 740), as well as in the following recent works, not cited by TISCHLER: MARCHAL 1920, TÄCKHOLM 1922, LJUNGDAHL 1922, AFZELIUS 1922, JØRGENSEN 1923 and GOODSPEED 1923. All numbers are haploids.

In the following genera most of the chromosome numbers represent multiples of a common fundamental number:

Rumex	8, 12, 16, ca. 24, 32, ca. 40.
Papaver	7, 14, 21, 35; 11, 22.
Rosa	7, 14, 21, 28 and many hybrids.
Primula	9, 12, 18, 24, 27; 11.
Solanum	12, ca. 18, 24, 36, 72.
Nicotiana	9, 12, 18, 24; 10.
Valeriana	16, 24, 32.
Erigeron	9, 18, 27; 13, 26.
Chrysanthemum	9, 18, 27, 36, 45.
Avena	7, 14, 21.
Triticum	7, 14, 21.
Hyacinthus	4, 8, 12 and many culture races with varying numbers.
Musa	8, 12, 16, 24; 11.

In the following genera, again, the chromosome numbers are somewhat more irregular, though multiples still occur.

Callitriche	3, 5, 10, 19.
Acer	11, 13, 26, 36, 54, ca. 72.
Viola	6, 12, 24, 36 (?); 10, 13, 17.
Campanula	8, 10, 13; 17, 34, 51.
Crepis	3, 4, 5, 6, 8, 9, 16, 21.
Lactuca	5, 7, 9; 8, 12, 16, 24.

It is seen that some genera have multiple numbers exclusively, in others, again, irregular numbers are found together with multiples. In some of the latter cases the irregular numbers are probably of secondary origin, apparently being the result of crosses between species with multiples *(Papaver, Primula, Erigeron, Musa* and perhaps *Viola).* In *Papaver* the number 11 is probably a result of a cross between a species with 7 and another with 14 chromosomes, but from this number 11 a new series of multiples has begun (11, 22). The same might perhaps be the case with *Erigeron,* though it is somewhat uncertain whether the 26-chromosome species really has that number or 27. In other genera the irregular numbers are the primitive ones, the multiples appearing only among the higher and, consequently, younger numbers *(Campanula, Crepis, Lactuca).*

Of many plant genera, only a few chromosome numbers are as yet known. The numbers known indicate, however, that these genera probably belong to the above-mentioned two categories. Thus in many genera only two numbers have been found of which one is the double or triple of the other, *e. g. Plantago* (6, 12), *Atriplex* (9, 18),

Drosera (10, 20) or *Platanthera* (21, 63). These cases probably represent parts of series like those above.

In several genera only one chromosome number has been found in many species. The most significant case is that of *Lilium,* of which 12 species have as yet been investigated, all having 12 chromosomes.

It is thus clear that *a quite unique position within the vegetable kingdom is as yet held by Carex,* where the following 22 *irregular* chromosome numbers have been found:

9, 15, 16, 19, 24, 25, 26, 27, 28, 29, 31, 32, 33, 34, 35, 36, 37, 38, 40, 41, 42 and 56.

That no really multiple (*i. e.* polyploid) numbers occur in this genus, has already been stated in chapt. 6.

Finally we state that a number of genera are characterized by apogamous or otherwise agamospermous (TÄCKHOLM 1922) species of hybrid origin, showing irregular reduction division and sometimes irregular chromosome numbers. To this category *Hieracium, Taraxacum* and *Rosa,* sect. *Caninae,* belong among others.

The review above shows that among the plant genera several different cytological types are found, though no quite sharp limits can be drawn between these types. It is, however, clear that they represent different types of species-formation, as the processes, through which new chromosome numbers have arisen, most certainly must have given rise to new species or races at the same time. Thus species with multiple numbers probably have arisen through a special process of bastardizing according to the scheme of WINGE (1917), while species with irregular numbers may have arisen through bastardizing, accompanied by irregular chromosome distribution in meiosis, or through mutations of the *Oenothera lata* type or perhaps through still some other processes that might have given rise to new and irregular chromosome numbers. In genera, again, that contain species all with the same chromosome number, the species-formation must have followed other lines. Here mutations within the chromosome or bastardizing, accompanied by regular Mendelian segregation, must have been the active processes. It seems, by the bye, — judging from the hybridization experiments of HERIBERT-NILSSON (1918) — highly probable that *Salix* belongs to this type of genera. In agamospermous genera, finally, bastardizing and mutations have been combined in a quite special way. It is, besides, probable that Mendelian segregations and mutations within the chromosomes often occur in combination with the other processes of species-formation. What we want to

point out is, however, that *the different processes of species-formation that have been acting in the vegetable kingdom have plaid a different rôle in different plant genera.* All attempts to explain the evolution of species with the aid of one formula only must necessarily fail, as there are several processes acting in nature. Thus Darwinism and Lamarckism as well as the Mutation theory of DE VRIES and the hybridization opinions of LOTSY or HERIBERT-NILSSON are all too extreme to contain the whole truth. It is necessary to realize that several species-creating processes act in nature and that their relative importance is different in different plant genera.

The considerations above refer to the origin of *species* and *specific* chromosome numbers only. As to the origin of *genera,* this latter problem is obviously intimately combined with the problem of the origin of the basic or fundamental numbers in the different genera. A genus is obviously a reality, not a mere abstraction. It is a phylum of species with a common origin, as shown by the chromosome numbers that often stand in clear relations to one another. Thus, in fact, a series of multiple numbers in a genus represents a piece of evolutionary history on a small scale and may be regarded as a fairly good illustration of the monophyletic origin of such a genus. In tracing — with the aid of the chromosomes — the phylogenetic relations between several genera, again, it is necessary to compare their basic numbers. We have, however, as yet not sufficient material for tracing the phylogeny of the basic numbers, and all speculations on a common fundamental number of larger groups, such as the phanerogams (*e. g.* MARCHAL 1920), seem to be, as yet, too early.

X. SUMMARY.

1. An introductory review is given of previous works on the cytology of *Carex,* critical remarks being made on the paper by STOUT (1913). It is stated that the chromosomes do not maintain their individuality in really resting nuclei. The stages, described by STOUT, were probably interphases. It seems quite excluded that the chromosomes in *Carex* are arranged in one single, continuous thread, as described by STOUT for *C. aquatilis.* It seems also highly improbable that the chromosomes of *C. aquatilis* should keep a spherical shape in all stages (except synezesis), as maintained by STOUT, because in other species they have the shape of rods or threads.

2. In table 1 (p. 134) the chromosome numbers of forty-four

species or forms are given. It appears that twenty-two different, exactly determined chromosome numbers have been found, *viz.* the following: 9, 15, 16, 19, 24, 25, 26, 27, 28, 29, 31, 32, 33, 34, 35, 36, 37, 38, 40, 41, 42 and 56. These numbers cannot be arranged in a series of multiples like those, now known from many plant genera.

3. As a rule, the chromosomes decrease in size when their number increases. This gradual decrease in chromosome size should be regarded as an expression of a limitation in the cells' capacity of producing chromatin.

Great differences in size are often found between chromosomes within the same nucleus. Exact measurements — according to a special method — have been made on the chromosomes of *C. pilulifera, panicea* and *ericetorum*. *C. pilulifera* has 3 long (A), 4 medium (B) and 2 short (C) chromosomes (haploid), *C. panicea* has 3 A, 2 B and 11 C chromosomes. In both species the length relation $A = B + C$ is found. This should probably be explained as a result of a transverse division of a long chromosome into a medium and a short one that has once taken place and given rise to the three size classes. *C. ericetorum* has 1 B + 14 C chromosomes. A comparison between these species shows that the length relations between the chromosomes (A : B : C) are the same in all the three species, except that the short chromosomes in *C. panicea* are relatively somewhat longer than in the other species. This means that the nuclei of these species probably contain homologous chromosomes what apparently holds good for the other *Carex*-species, too. Large and small chromosomes have been found in several other species as well (table 5, p. 157).

4. A few cases of irregular chromosome distribution in meiosis are described.

5. Relations between chromosome numbers and taxonomy in *Triticum, Campanula, Primula, Lactuca, Rosa, Viola, Chrysanthemum* and in *Anthemideae* and *Heliantheae,* according to previous works by other writers, are discussed and the following results are obtained: In some of the above-mentioned genera, where multiple chromosome numbers occur, it is found that nearly related species have the same chromosome number, in others, again, different sections of the genus are characterized by different series of, as a rule, multiple numbers, related species belonging to the same series. The *Caninae*-section of the genus *Rosa* offers a special case. Among animals similar relations have been found in *Cyclops,* where nearly related species have adjacent chromosome numbers. Several greater animal groups (*e. g.* the

Orthopteran family *Acrididae*) show a remarkable constancy in chromosome number. All evidence, hitherto brought together, shows that the chromosome number of a given species is, as a rule, constant.

In *Carex* the following results have been obtained: A few instances investigated show that the chromosome number of a species is the same in different localities. It has further been found that species, belonging to the same section of the genus *Carex,* have numbers of about the same height. Groups of adjacent chromosome numbers are obtained, when the species are arranged according to systematic relationships (table 6). As this relation has been found to hold good in all cases, hitherto investigated, it seems allowable to make the additional statement that the chromosome numbers of a group of related species may be approximately estimated, when the number of one species of the group is known.

6. The meaning of the word polyploid is discussed. According to the present writer a polyploid species is a species, the nuclei of which contain a multiple of haploid sets, all with the same number of chromosomes, though it is not necessary that these sets should be identical from a genetical point of view.

The chromosome numbers in *Carex* are irregular: it has not been possible to find the slightest vestiges of any series of multiples. There is further no fixed relation, constant for all species, to be found between the number of chromosomes of the different size classes. From these facts is concluded that polyploidy does not occur in the genus *Carex.*

The problem of transverse division of chromosomes is discussed. It is stated that such divisions have been found in several cases. It is pointed out that transverse divisions may take place in single chromosomes but most certainly not in whole sets simultaneously. As to *Carex,* transverse division of a long chromosome, through which a medium and a short one have arisen, probably has taken place at the formation of the original, fundamental set of the genus. Whether it has contributed to the formation of the higher numbers in the genus, too, is difficult to decide but it does not seem improbable.

Generally the higher numbers in *Carex* must have arisen through duplication of entire chromosomes. This evolution of new numbers must have been a process of gradual changes, each number probably having arisen from the nearest lower number. The systematic distribution of the numbers is unexplainable under the assumption of sudden great changes in chromosome number. The essential part of the

process has apparently been the origin of univalent chromosomes that have divided longitudinally in meiosis and thus given rise to gametes with extra chromosomes. These univalents have probably arisen through lacking conjugation. Non-disjunction, too, may have played a rôle in the evolution of new numbers. Several considerations (cf. p. 185) render it probable that the evolution of the chromosome numbers in *Carex* has gone from low numbers to higher ones, or that the lowest numbers are the oldest and most primitive ones, while the highest numbers are the youngest. The writer's opinions on the evolution of the chromosome numbers in *Carex* are summarized on p. 187.

7. As to the species-formation in *Carex,* one of the most important processes has apparently been the formation of mutants with one extra chromosome (*Oenothera lata*-type) which, in a later generation, have given rise to mutants with the diploid number increased by two. Mutational changes within the chromosomes have probably also been of importance, as well as hybridizations, though the latter process, according to the opinions of the writer, does not seem to have played any greater rôle.

8. The chromosome numbers must be of great importance in all attempts to trace the phylogeny of the genus *Carex.* All phylogenetical lines must be drawn from groups with low numbers to those with higher ones.

It appears from table 1 (p. 134) that *Montanae* and *Paniceae* are the most primitive sections of the genus hitherto investigated by the writer. It is probable that *Acutae* has descended from *Atratae.* It seems, as if a phylogenetic line, characterized by great differences in chromosome size, might be drawn as follows: *Paniceae* → *Trachychlaenae* → *Atratae* → *Acutae.* The following sections which apparently form a natural phylum are young: *Pseudo-cypereae, Physocarpae, Paludosae* and *Hirtae.* The evolution within *Eucarex* has gone from small to large and coarse species and from dry soil into swamps and bogs.

Vignea is regarded by systematists as a more uniform subgenus than *Eucarex.* This is confirmed by the chromosome numbers that seem to be less variable than in *Eucarex. Vignea* appears to be a subgenus of mean age.

The chromosome numbers show that *Dioicae* and *Petraeae* cannot be any very primitive groups, but that they may very well be related to *Elongatae* and *Digitatae* resp.

A diagram of the phylogenetic views, developed in the present work, is given in fig. 13 (p. 197).

An attempt is made to test the Age and Area hypothesis of WILLIS by means of the chromosome numbers in *Carex*, but no conclusive results are obtained.

9. Some plant genera are classified from the point of view of their chromosome numbers. Some of these genera have multiple numbers exclusively, in others irregular numbers are found together with multiples. In some genera only one chromosome number has been found in many species. The genus *Carex*, of which 22 irregular chromosome numbers are known, occupies a unique position within the vegetable kingdom. These different cytological types of genera represent different types of species-formation.

Botanical Institute, University of Stockholm, February 1924.

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DESCRIPTION OF PLATE I.

Photo-micrographs of chromosomes in the pollen-development of *Carex*-species. Photographs not retouched. — The plates used were Ilford half-tone plates, in fig. 4—12 after development intensified with uranic intensifier, all copied on Cyko (mostly contrast) paper. — Fig. 1: ZEISS hom. imm. $^1/_{17}$, comp. oc. 4, length of camera 95 cm (× 750). Fig. 2: LEITZ hom. imm. $^1/_{16}$, ZEISS comp. oc. 6, length of camera 70 cm (× 1700). Fig. 3: ZEISS hom. imm. $^1/_{17}$, comp. oc. 8, length of camera 95 cm (× 1500). Fig. 4—12: LEITZ hom. imm. $^1/_{16}$, ZEISS comp. oc. 8, length of camera 95 cm (× 3300).

Fig. 1. Pollen-sac of *C. pilulifera* with pollen-nuclei in prophase. — Fig. 2. Pollen-tetrad of *C. panicea* with nuclei in prophase. The surviving nucleus and two of the degenerating are seen. — Fig. 3. Pollen-sac of *C. Hornschuchiana* with heterotypic metaphases in P. M. C. — Fig. 4. Heterotypic metaphase in P. M. C. of *C. pilulifera* (X = 9, same as textfig. 1 a). — Fig. 5. Ditto of *C. panicea* (X = 16, same as textfig. 5 b). — Fig. 6. Ditto of *C. sparsiflora* (X = 16, same as textfig. 10 a). — Fig. 7. Ditto of *C. montana* (X = 19, same as textfig. 10 f). — Fig. 8. Ditto of *C. loliacea* (X = 27). — Fig. 9. Ditto of *C. Hornschuchiana* (X = 28, same as textfig. 1 n). — Fig. 10. Ditto of *C. distans* (X = 37, same as textfig. 2 i). — Fig. 11. Ditto of *C. vesicaria* (X = 41, same as textfig. 2 m). — Fig. 12. Ditto of *C. hirta* (X = 56, same as textfig. 2 p).

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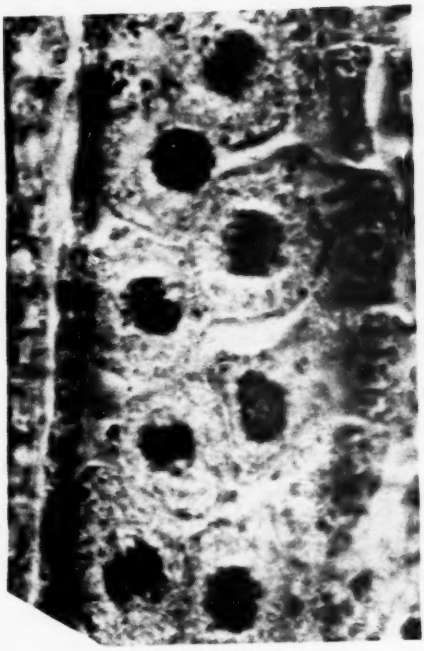

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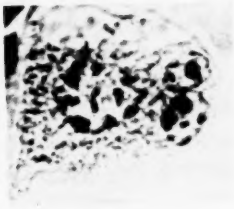

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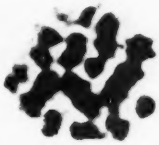

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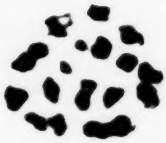

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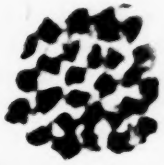

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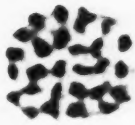
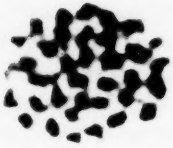


9



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11

12

O. Heilb. Photo.

ÜBER EINE EIGENARTIGE ÄHREN-ANOMALIE BEI WEIZEN

VON *BIRGER KAJANUS*
LANDSKRONA, SCHWEDEN

ZIEMLICH oft habe ich bei Weizen auf Weibullsholm eine Anomalie gefunden, die darin besteht, dass in den Ähren ausser typischen Ährchen besondere Ährchenbildungen vorkommen. Diese Bildungen haben ein sehr wechselndes Gepräge (Fig. 1): es gibt allerlei Stufen von relativ gut entwickelten Ährchen, die ein oder zwei Körner enthalten, bis schmale Rudimente, die nur aus einer deformierten Klappe bestehen. Die Adventivbildungen sitzen immer einzeln unmittelbar unter normalen Ährchen, von deren Basis sie ausgehen; bei Vorhandensein mehrerer solcher Bildungen in einer Ähre sitzen dieselben bei angrenzenden Ährchen. Wenn die Adventivbildungen verhältnismässig gross sind und die typischen Ährchen nicht besonders dicht sitzen, lässt sich sofort erkennen, dass die Achse der Adventivbildungen mit derjenigen der eigentlichen Ährchen einen rechten Winkel bildet, und dass die Breitenflächen der Adventivährchen diejenigen der normalen Ährchen kreuzen. Bei geringerer Entwicklung der Adventivbildungen und bei gedrängterer Stellung der normalen Ährchen sind diese Verhältnisse weniger deutlich.

Die betreffende Anomalie wurde von mir in verschiedenen Jahren und bei Materiale verschiedener Herkunft angetroffen, aber fast ausschliesslich bei *Triticum vulgare*. Nur in der F_3-Generation einer Kreuzung zwischen *vulgare* (Idunaweizen) und *Spelta* (Sortennamen unbekannt) wurde sie in seltenen Fällen auch bei spelzartigen Individuen (wahrscheinlich Heterozygoten) beobachtet, dabei aber nur in der Form steriler Bildungen. Unter den F_3-Beständen dieser Kreuzung, die im Jahre 1914 geerntet wurden, fanden sich nicht wenige, bei denen die erwähnte Anomalie vorhanden war, ausser in den genannten Fällen jedoch nur bei *vulgare*-Pflanzen, dabei aber sowohl in konstanten *vulgare*-Beständen als auch in Spaltungsbeständen. Meistens trat die Anomalie nur bei einzelnen Individuen auf, in gewissen Beständen kamen indessen mehrere, sogar viele aberrante Pflanzen vor. In einem konstanten *vulgare*-Bestande waren 37 Pflanzen normal und 4 aber-

rant, in einem anderen 32 normal und 28 aberrant; in einem Spaltungsbestande befanden sich unter den *vulgare*-Individuen 9 normale und 5 aberrante, in einem anderen 3 normale und 8 aberrante.

Fig. 1. Drei Ähren mit Adventivährchen. Sämtliche Ähren sind ein und derselben Pflanze entnommen. — Nat. Grösse.

In der besprochenen F_3-Generation kam in einem Falle, in einem Spaltungsbestande, unter 20 *vulgare*-Pflanzen ein aberrantes Indivi-

duum vor, bei dem die Anomalie zudem relativ stark ausgeprägt war. Diese Pflanze, die drei Ähren hatte, sämtlich mit abnormen, z. T. fertilen Ährchenbildungen (Fig. 1), wurde verfolgt, wobei alle Körner, diejenigen der fertilen Adventivährchen von denjenigen der normalen Ährchen getrennt, einzeln gesät wurden. Nach den Körnern der normalen Ährchen (Kornzahl nicht ermittelt) wurden 61 Pflanzen gezogen, von denen 5 mit wenigen, meistens sterilen Adventivbildungen versehen waren; nach den 8 Körnern der Adventivährchen der Mutterpflanze wurden 4 Pflanzen erzielt, von denen eine die betreffende Anomalie zeigte. Aus diesem Resultate ist zu schliessen, dass die Anomalie vererbt wurde, obwohl sie nur bei wenigen Nachkommen erschien; diese Spärlichkeit im Auftreten dürfte darauf beruhen, dass gewisse für die Ausbildung der Anomalie notwendige Bedingungen nur in geringem Grade vorhanden waren. Die Vererbung war nach Körnern aus den aberranten Ährchen dem Anschein nach nicht stärker als nach solchen aus den normalen Ährchen; anders war auch kaum zu erwarten.

Ich habe in der Literatur einige Angaben gefunden, die sich auf identische oder ähnliche Bildungsabweichungen beziehen; da die betreffenden Angaben zur weiteren Beleuchtung der diskutierten Erscheinung dienen können, werden sie im folgenden wiedergegeben.

Unter der Rubrik »Verdoppelung der Ährchen über einander» teilt KÖRNICKE mit (1885, S. 29—30), dass er eine solche Bildungsabweichung bei verschiedenen *vulgare*-Sorten angetroffen hat. Laut ihm »treten alljährlich Ähren auf, an welchen sich unmittelbar unter einem oder mehreren Ährchen ein zweites kleineres Ährchen befindet, welches nach aussen oder zurückgekrümmt ist. Es ist bald grösser, bald kleiner, sehr selten mit einem Korne, nicht selten nur auf ein klappenartiges Blättchen reduciert.». — »Sie sind insofern samenbeständig, als immer ein Teil der Ernte die gleiche Erscheinung zeigt. Dabei ist es gleichgültig, ob man zur Aussaat die Körner aus diesen oder aus einfachen Ähren nimmt. Bei mehrjähriger Aussaat der ersteren nahm die Anzahl der gleichen Ähren nicht zu. In einem Jahre traten wenig, in einem anderen viele auf. Einmal trugen über die Hälfte der Ähren Doppelährchen.»

Diese Angaben beziehen sich auf drei unbegrannte Sorten. »Etwas anders zeigten sich die über einander gestellten Doppelährchen bei drei Ähren eines begrannten Sommerweizens. Das untere Ährchen war in die Höhe gerichtet, gut ausgebildet und mit guten Früchten. Bei Aussaat derselben trat aber diese Erscheinung nicht wieder ein.»

MEUNISSIER schreibt (1918, S. 16): »Epillets surnuméraires. — Anomalie curieuse dans laquelle on observe la tendance à produire deux épillets en un même point du rachis, ou même leur développement complet. Cette anomalie a été observée sur diverses variétés de Blé tendre sans barbes, surtout depuis 1900; quoiqu'elle soit d'origine ancienne, ainsi que le montre un épi de la variété »Van Diemen» cultivé à Verrières en 1852, présentant un épillet surnuméraire parfaitement développé. Cette variété est encore, à l'heure actuelle, une de celles qui produit le plus fréquemment cette curieuse particularité.

Dans les croisements, l'anomalie se comporte comme récessive, mais il y a des gradations diverses et on a pu distinguer dans la même variété (Chiddam d'automne à épi blanc × Gros bleu) une race pauvre en épillets surnuméraires et une race riche.»

MEUNISSIER hat zwei Typen abgebildet, von denen der eine begrannt, der andere unbegrannt ist; bei jenem scheinen wenige, bei diesem viele Adventivährchen vorzukommen. Diese Adventivährchen haben augenscheinlich dieselbe Stellung wie in den von mir beobachteten Fällen.

PERCIVAL spricht von »supernumerary spikelets» und sagt u. a. (1921, S. 359): »Additional spikelets are frequently found growing from the rachis immediately below the points of insertion of the normal spikelets and generally arranged parallel to them» (wie eine beigefügte Abbildung zeigt). »In some cases they produce one or two grains, but are often rudimentary, consisting only of minute misshapen glumes. These variations occur chiefly in ears of the latest tillers, the ears which develop first being usually quite normal; the variation does not appear every season, though a form which has once shown it may produce it again.» PERCIVAL fand die Anomalie besonders bei chinesischen *vulgare*-Sorten.

Ein Unterschied im Auftreten der Anomalie je nach der Entwicklungszeit der Halme in Übereinstimmung mit der Angabe PERCIVAL'S ist von mir nicht beobachtet worden.

Zuletzt ist VAVILOV zu erwähnen, der sich in seiner neulich erschienenen, vorzüglichen Abhandlung über die Systematik von *Triticum vulgare* (1923) in folgender Weise äussert (S. 236): »For some races the development of additional spikelets at the base of the normal ones is characteristic.» Bei seiner Gruppierung der Merkmale laut dem Grade ihres systematischen Wertes führt er die betreffende Anomalie zu denjenigen Charakteren, die die geringste systematische Bedeutung haben. Es handelt sich dabei um »very much fluctuating

features greatly depending on outward conditions. The races are only distinguishable when sown under like conditions and even for some consecutive years, which alone makes determination of characters of races possible» (S. 245).

Aus den obigen Mitteilungen geht folgendes hervor. Die Bildung von Adventivährchen kommt bei *Triticum vulgare* ziemlich häufig vor; die Anomalie ist erblich und zwar rezessiv, in bezug auf ihre Entwicklung und Ausbreitung aber teils von der sonstigen genetischen Beschaffenheit der Rasse (KÖRNICKE, MEUNISSIER), teils von äusseren Umständen abhängig. Die Adventivährchen sitzen entweder quer im Verhältnis zu den normalen Ährchen (wie in den von mir beobachteten Fällen) oder sie sind mit diesen möglichst parallel (PERCIVAL). Die verschiedene Stellung der Adventivährchen ist wohl mit verschiedener Veranlagung verknüpft, indessen lässt sich diese Frage natürlich erst durch spezielle Untersuchungen entscheiden.

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KREUZUNGSKLEINIGKEITEN

VERSUCHE MIT CAPSELLA BURSA PASTORIS, LACTUCA MURALIS, FAGOPYRUM EMARGINATUM, GERANIUM ROBERTIANUM, GEUM RIVALE, DRACOCEPHALUM THYMIFLORUM UND NICANDRA PHYSALOIDES

VON *K. V. OSSIAN DAHLGREN*
UPPSALA

UNTER dem Titel Kreuzungskleinigkeiten habe ich einige kleinere Untersuchungen vereinigt. Es sind teils Ergänzungen früherer Untersuchungen, teils Versuche die mehr gelegentlich mit verschiedenen Pflanzen angestellt worden sind.

I. CAPSELLA BURSA PASTORIS.

In einer vorhergehenden Abhandlung (DAHLGREN 1919) habe ich gezeigt, dass eine (dekandrische) apetala-Form von *Capsella bursa pastoris* mit der bekannten *C. Heegeri* gekreuzt, in Bezug auf Kapselform eine Spaltung in 15 Normalfrüchtige auf 1 *Heegeri* in F_2 aufweist. Dasselbe hat vorher SHULL (1914) bei seinen Kreuzungen zwischen normalen *Capsella*-Formen und dem *Heegeri*-Typus gefunden. Da ich glaubte früher (DAHLGREN 1915) eine Spaltung im Verhältnis 3 : 1 beobachtet zu haben, habe ich gelegentlich noch eine Kreuzung mit *Heegeri* gemacht. Als Vaterpflanze benutzte ich ein Exemplar von der biologischen Meeresstation zu Kristineberg, Westküste Schwedens, welches von Herrn Professor Dr. E. ALMQUIST als die »Elementarart» *C. perhians* bestimmt worden ist (siehe ALMQUIST 1921, S. 89).

Wie vorausgesehen hatten die F_1-Pflanzen alle herzförmige Früchte. In F_2 traten folgende Spaltungen ein:

1)	13	*normalfrüchtig*	und	1	*Heegeri*
2)	59	»	»	2	»
3)	79	»	»	2	»
4)	87	»	»	9	»
Summe	238	*normalfrüchtig*	und	14	*Heegeri*
Verhältnis pro 16:	15,111	»	»	0,888	»

Abweichung 0,111; Mittlerer Fehler $\pm$ 0,244.

Bei *C. perhians* sind folglich auch zwei homomere Faktoren (von dem Typus, den SHULL »duplicate genes» genannt hat) für die dreieckige Kapselform vorhanden.

Ein *Heegeri*-Individuum, mit einer anderen, leider nicht näher bestimmten *Capsella*-Pflanze von Kristineberg gekreuzt, gab in F_2:

	Normalfrüchtig	*Heegeri*
1)	49	2
2)	38	4
Summe	87	6

Folglich trat auch hier eine besonders schöne Spaltung nach dem Verhältnis 15 : 1 ein.

Eine F_2-*Heegeri*-Pflanze nach meiner Kreuzung *C. Heegeri* × *apetala* (DAHLGREN 1919) war offenbar heterozygotisch (*Ee*) in Bezug auf den Blumenblattfaktor. In F_3 erhielt ich, wie erwartet, eine — jedoch nicht so schöne — Spaltung nach Ratio 3 : 1, wenn ich (aus vorher erwähnten Gründen) die *EE*- und *Ee*-Individuen zu derselben Gruppe zählte:

Gefunden 57 *E* und 27 *e*
Berechnet pro 4: 2,714 » » 1,286 »
Abweichung 0,286; Mittlerer Fehler ± 0,189.

II. LACTUCA MURALIS.

Bei der Kreuzung dieser Art mit einer *atropurpurea*-Form habe ich gefunden, dass die dunkelrote Farbe rezessiv ist (DAHLGREN 1918,

F_2-Fam.	Anzahl Individuen		Summe	Verhältniszahlen pro 4	Differenz D	Mittlerer Fehler m_k	D/m_k
	normal	*atropurpurea*					
1	316	98	414	3,053 : 0,947	0,058	± 0,085	0,62
2	307	110	417	2,945 : 1,055	0,055	± 0,085	0,65
3	192	58	250	3,072 : 0,928	0,072	± 0,110	0,66
4	148	38	186	3,183 : 0,817	0,183	± 0,127	1,44
5	91	32	123	2,959 : 1,041	0,041	± 0,156	0,26
6	62	23	85	2,918 : 1,082	0,082	± 0,188	0,44
7	7	2	9	3,111 : 0,999	0,111	± 0,577	0,19
1—7	1123	361	1484	3,027 : 0,973	0,027	± 0,045	0,6

S. 109) und dass in F_2 eine Spaltung in 471 grün und 138 rotbraun stattgefunden hat.

Von der umgekehrten Kreuzung, also *atropurpurea* × Normaltypus, habe ich die obenstehenden F_2-Familien gezüchtet, die ja auch, wie erwartet, eine gewöhnliche Spaltung demonstrieren.

III. FAGOPYRUM EMARGINATUM.

Ein selbstbefruchtetes, kurzgriffliges Exemplar dieser Art ergab 10 gleichfalls kurzgrifflige Abkömmlinge, obwohl man erwarten konnte, dass wenigstens ein Exemplar langgrifflig sein werde. Hierüber habe ich (DAHLGREN 1922, S. 95) folgende Bemerkung gemacht: »Ob dies ein Zufall oder ob die genannte Pflanze ein Homozygot ist, durch eine spontane illegitime Pollination entstanden, kann man natürlich leicht entscheiden, indem man nächstes Jahr die zahlreichen Samen aussät.» Ich hatte nämlich alle zehn Abkömmlinge dicht nebeneinander angepflanzt und zwar in einer Gegend (Sala), wo keine Buchweizenpflanzen vorhanden waren und erhielt dabei, trotz Mangel an langgriffligen Exemplaren, einen recht guten Fruchtansatz.

Die erhaltenen Früchte, zusammen ausgesät, gaben 148 Individuen, von denen

118 *kurzgrifflig* und 30 *langgrifflig* waren.

Die ursprüngliche Pflanze war also heterozygotisch. Unter der Voraussetzung, dass alle die 10 kurzgriffligen Abkömmlinge genau zur selben Zeit blühten, mit demselben Reichtum, und dass keine »Zertation» zwischen den Pollenschläuchen vorhanden sei, würden wir in der nächsten Generation verschiedene Zahlenverhältnisse erhalten, je nach den Proportionen zwischen *AA*- und *Aa*-Individuen unter den Eltern. Für drei Fälle sind die Zahlen hier unten ausgerechnet:

Elternpflanzen	Gametenproportion	Theoretische Verhältniszahlen der Abkömmlinge	Auf 148 berechnet	Mittlerer Fehler
$4\,AA + 6\,Aa$	$7\,A : 3\,a$	91 : 9 (etwa 10 : 1)	$134{,}68 : 13{,}32$	$\pm 3{,}48$
$3\,AA + 7\,Aa$	$13\,A : 7\,a$	351 : 49 (etwa 7 : 1)	$129{,}87 : 18{,}13$	$\pm 3{,}99$
$2\,AA + 8\,Aa$	$3\,A : 2\,a$	21 : 4 (etwa 5 : 1)	$124{,}32 : 23{,}68$	$\pm 4{,}46$

Die gefundenen Zahlen waren wie gesagt 118 : 30. Es hat aber wenig Zweck, über diese Sachen zu theoretisieren, da ja die oben vorausgesetzten Bedingungen kaum alle erfüllt waren. (Ich nehme

hier die Gelegenheit wahr, auf vier neue Arbeiten von LAIBACH, STOUT, BARLOW und Fräulein v. UBISCH aufmerksam zu machen, welche im Jahre 1923 erschienen sind. Es wird darin die Heterostylie bei *Linum, Lythrum, Oxalis* und *Primula* behandelt.)

IV. GERANIUM ROBERTIANUM.

Von dieser Art gibt es eine Form mit weissen anstatt rosenroten Blüten, f. *leucanthum*, welche sich als konstant erwiesen hat. Im Jahre 1918 habe ich bei Engelsberg in Västmanland (eine schwedische Provinz) ein einziges weissblühendes Exemplar, unter der Hauptart wachsend, gefunden.

Diese *leucanthum*-Form habe ich mit der Hauptart gekreuzt. F_1 war rotblühend.

Mit der Kultur von *Geranium robertianum* habe ich recht viel Mühe gehabt. Während des ersten Jahres entwickeln sich ganz ausserordentlich kräftige Rosettenpflanzen, welche jedoch später bei der Überwinterung grösstenteils zu Grunde gehen. Ich habe deshalb nur wenige blühende F_2-Exemplare erhalten. Offenbar tritt eine monohybride Spaltung ein, wie aus untenstehender Übersicht hervorgeht:

1)	3	*rot*	und	1	*weiss*
2)	6	»	»	3	»
3)	7	»	»	2	»
4)	10	»	»	2	»
Summe	26	*rot*	und	8	*weiss*
Berechnet	25,5	»	»	8,5	»

V. GEUM RIVALE.

Seit langer Zeit kennt man eine *Geum rivale* nahestehende »Art», *G. pallidum* C. A. MEYER genannt, die kein Anthozyan hat. Besonders auffallend sind die Unterschiede während und nach dem Blühen, wo Blumenstiel, Kelch und Früchte bei diesem gelblichgrün sind, dagegen bei jenem bekanntlich mehr oder weniger ausgesprochen rotbraun. *G. pallidum* hat ausserdem weissliche Blumenblätter. Eine Vorstellung von dem Unterschied zwischen den beiden Typen kann man sich vielleicht nach einer gewöhnlichen Photographie machen (Fig. 1).

Fig. 1. *Geum pallidum* links; *G. rivale* rechts.

Diejenigen *pallidum*-Exemplare, welche ich zur Kreuzung mit *G. rivale* benutzt habe, stammen aus dem hiesigen botanischen Garten, wo sie seit Jahren kultiviert sind. Ich habe gefunden, dass *G. pallidum* bei Inzucht völlig konstant ist. Dasselbe hat übrigens schon SCHEUTZ (1870, S. 39) festgestellt.

Geum pallidum mit *G. rivale* gekreuzt, gab eine rotbraune F_1, die jedoch etwas heller war als die Vaterpflanze. Da es nicht immer so leicht war in F_2 die Heterozygoten von den homozygotischen rotbraunen Individuen zu unterscheiden, habe ich die *AA*- und *Aa*-Pflanzen zusammengezählt. Wie nachstehende Tabelle ersichtlich macht, findet eine gewöhnliche monohybride Spaltung statt.

F_2-Fam.	Anzahl Individuen		Summe	Verhältniszahlen pro 4	Differenz D	Mittlerer Fehler m_k	D/m_k
	rivale	*pallidum*					
1	91	40	131	2,779 : 1,221	0,221	± 0,151	1,46
2	83	19	102	3,255 : 0,745	0,255	± 0,171	1,49
3	82	27	109	3,009 : 0,991	0,009	± 0,166	0,05
4	47	21	68	2,765 : 1,235	0,235	± 0,210	1,12
5	43	18	61	2,820 : 1,180	0,180	± 0,222	0,81
6	29	10	39	2,974 : 1,026	0,026	± 0,277	0,09
7	16	2	18	3,556 : 0,444	0,556	± 0,408	1,36
1—7	391	137	528	2,962 : 1,038	0,038	± 0,075	0,50

MURBECK (1894, S. 14) hat den Bastard *Geum pallidum* × *urbanum* beschrieben, welcher im Bergianischen Garten, Stockholm, ent-

standen ist. Diese Pflanze unterscheidet sich von dem gewöhnlichen *G. rivale* × *urbanum* nur durch eine blassere Farbe der Blütenteile.

Sämtlichen Verfassern, welche sich mit *G. pallidum* beschäftigt haben, ist natürlich dessen nahe Verwandtschaft mit *G. rivale* aufgefallen. MURBECK betont auch, jedoch ohne »ein bestimmtes Urteil» abgeben zu wollen, dass *G. pallidum* vielleicht als eine »dann und wann entstehende Abänderung des *G. rivale*» anzusehen sei. Ohne Zweifel ist auch das sog. *G. pallidum* nur eine Form unsrer gewöhnlichen Bach-Nelkenwurz. Bei Kreuzung findet ja eine monohybride Spaltung statt, und da ist es — wie ich schon betont habe (DAHLGREN 1924, S. 20) — wohl am zweckmässigsten sie systematisch nicht als verschiedene Spezies zu betrachten.

VI. DRACOCEPHALUM THYMIFLORUM.

In einer Saat von obenstehender Pflanze fanden sich zwei Individuen vor, welche durch ihre Farbe schon von weitem in die Augen fielen. Sie waren nämlich hellgrün, weissblühend und total ohne

F_2-Fam.	Anzahl Individuen		Summe	Verhältniszahlen pro 4	Differenz D	Mittlerer Fehler m_k	D/m_k
	typica	*pallida*					
1	364	121	485	3,002 : 0,998	0,002	± 0,079	0,03
2	358	124	482	2,971 : 1,029	0,029	± 0,079	0,37
3	310	118	428	2,897 : 1,103	0,103	± 0,084	1,23
4	294	108	402	2,925 : 1,075	0,075	± 0,086	0,86
5	228	69	297	3,071 : 0,929	0,071	± 0,101	0,70
6	215	51	266	3,233 : 0,767	0,233	± 0,106	2,19
7	211	76	287	2,941 : 1,059	0,059	± 0,102	0,58
8	144	49	193	2,984 : 1,016	0,016	± 0,125	0,13
9	75	21	96	3,125 : 0,875	0,125	± 0,177	0,71
10	49	12	61	3,211 : 0,789	0,211	± 0,222	0,95
11	27	9	36	3,000 : 1,000	0,000	± 0,289	0,00
12	19	6	25	3,040 : 0,960	0,040	± 0,346	0,12
1—12	2294	764	3058	3,001 : 0,999	0,001	± 0,031	0,02

Anthozyan. Die Hauptform dagegen ist blaublühend und ihre vegetativen Teile sind reich anthozyanführend. Das Abkommen der hellgrünen Exemplare — wir können sie f. *pallida* nennen — erwies sich als konstant. Schon im Keimpflanzstadium konnte man ohne Schwierigkeit die *pallida*-Individuen von denjenigen der Hauptform unter-

scheiden. Bei den letzteren werden nämlich die Hypocotyle und die untere Seite der Keimblätter schon frühzeitig anthozyanführend.

Die *pallida*-Form mit dem Normaltypus gekreuzt gab F_1-Pflanzen, welche dem letzteren völlig ähnlich waren. Es fanden in F_2 schöne monohybride Spaltungen statt, wie aus obenstehender Tabelle hervorgeht. Alle F_2-Familien, mit Ausnahme der Familien 9—12, sind im Keimpflanzstadium gezählt worden. Ganz erstaunlich fein sind ja die Summa Summarum-Zahlen; gefunden 2294 : 764; berechnet 2293,5 : 764,5 (!).

VII. NICANDRA PHYSALOIDES.

Die Petalen dieser Pflanze haben an der Basis einen deutlich markierten Fleck, welcher — schon im Knospenstadium bemerkbar — eine verhältnismässig kräftige blaue Farbe hat (Fig. 2, links). In einem Beet, wo *Nicandra physaloides* gesät war, traten ein paar Indi-

Fig. 2. *Nicandra physaloides.* Links f. *typica*; rechts f. *immaculata.*

viduen ohne Flecken auf (Fig. 2, rechts). Sie erwiesen sich als konstant, und diese Pflanzen will ich im Folgenden f. *immaculata* nennen.

Die F_1-Abkömmlinge der Verbindung *immaculata* × *typica* zeigten Dominanz der letzterwähnten Form. Die zahlreichen Pflanzen habe ich zusammen abblühen lassen. Sie gaben eine Menge Samen. Nächtes Jahr (1923) wurden Samen von dreissig Exemplaren im Garten ausgesät. Auf Grund verspäteter Aussaat und ungünstiger Witterungsverhältnisse haben sich die F_2-Pflanzen in allgemeinen ziemlich schlecht entwickelt. Sobald ein Exemplar blühte, ist es ausgezogen und registriert worden. *Nicandra physaloides* ist sehr empfindlich gegen Kälte, und schliesslich hat eine Frostnacht Hunderte von Exemplaren, welche noch nicht geblüht hatten, zerstört. Hier unten folgt eine Übersicht der gefundenen Zahlen:

Feldnummer	*typica*	*immaculata*	*Feldnummer*	*typica*	*immaculata*
1)	14	4	16)	5	0
2)	51	23	17)	41	11
3)	21	7	18)	25	9
4)	4	11	19)	9	8
5)	12	3	20)	16	5
6)	32	14	21)	14	0
7)	47	9	22)	14	6
8)	17	3	23)	13	6
9)	47	20	24)	12	4
10)	16	2	25)	9	3
11)	18	7	26)	14	9
12)	15	2	27)	19	4
13)	28	12	28)	11	6
14)	27	14	29)	11	2
15)	10	2	30)	11	3

Die Summa Summarum sämtlicher Pflanzen ist 792 wovon:

Gefunden: 583 *typica* und 209 *immaculata*
Berechnet: 594 » » 198 »
Differenz: 11; mittlerer Fehler $\pm$ 12,186.

Die Abweichung liegt innerhalb der Grenzen des mittleren Fehlers für eine monohybride Spaltung, also eine gute Übereinstimmung. Die Zahlenverhältnisse sind nicht immer so gut, wenn man die verschiedenen Feldnummern einzeln durchsieht. Zu bemerken ist jedoch, dass sie im allgemeinen verhältnismässig wenige Pflanzen umfassen. Die Abweichung ist auch, abgesehen von No. 4, immer geringer als der dreifache mittlere Fehler.

Uppsala, Botanisches Institut, Neujahr 1924.

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SOME REMARKS ON THE PRINCIPLES IN INBREEDING

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IN the report of the International Congress of Cattle-Breeders at the Hague 1923 (see Section I a) Professor TUFF calls attention to the fact that in livestock breeding the most difficult task is the attainment of homozygosity in the inheritable factors, which form the genotypic basis of the characteristics and capacities attained through the selection of animals.

In this essay I have used the term breed synonymously with the word population. In my opinion, a breed can *a priori* not be inbred by any of the methods which SEWALL WRIGHT refers to in his essays, mentioned by TUFF (1923), because nowadays in the coöperative breeding in most cases sires obtained from different breeders are used. The sires in question represent different female strains, therefore, if they are results of consanguineous matings, the sires in their pedigrees must exhibit an inbreeding carried on in a varying, more or less close, form and due to various ancestors. Matings of halfbrothers and sisters, recommended by TUFF, cannot according to SEWALL WRIGHT'S hypothesis be reckoned among the grossest forms of inbreeding. This method, however, can only be carried on in succeeding generations and with many difficulties within a stud or a large herd of cattle belonging to one owner, but not in the coöperative breeding. In the well-known Austrian stud Kladrub this *modus operandi* has been employed for a number of years. According to the above-mentioned reasons a breed cannot be inbred by continued matings of halfbrothers and sisters. A splitting up — in the genetic sense — into homozygotic lines cannot, therefore, come under consideration, as asserted by TUFF and SEWALL WRIGHT.

Inbreeding in the livestock history has as a rule been carried on in quite another way than by the methods practised in SEWALL WRIGHTS experiments and, in future livestock breeding, this will no doubt also remain so. In SEWALL WRIGHT'S experiments inbreeding and production of homozygotes are the starting point but not selec-

tion, whereas in livestock-breeding the reverse holds true. Production of homozygotes, as TUFF mentions, is one type of inbreeding, but quite another type in my opinion is the utilization through inbreeding of prepotent (homozygotic) individuals, when these now and then appear in a breed. These two types are not of quite the same importance. As regards inbreeding in livestock, only the latter type is of practical value.

Individuals belonging to a distinct breed have certain peculiarities in common including both external appearance and physiological capacities, both being inheritable and acquired through selection. There seems at present to be no dispute that the marked type of external appearance in a livestock-breed, save somatic influence, must be assumed to have a common origin to all its members, and chiefly due to inbreeding in a more or less close form. The history of livestock again and again tells us that in a breed remote inbreeding has occurred and that it has sprung from one or only a few superior animals belonging as a rule to the first period of the foundation of the breed. The said form of inbreeding is a natural consequence of the circumstance that these remote ancestors have produced at their time the best offspring, both sons and daughters, and so on in the following generations. Genealogical studies carried on in several countries seem to corroborate the correctness of these considerations. The said form of inbreeding which we might call a »concentration of the blood from a common progenitor» can be significant even if the common ancestor be dead long ago. The following examples will clearly show this fact.

»Generale Forata» in Kladrup.

(cp. DE CHAPEAUROUGE.)

One of the oldest common ancestors in the ancestry of this sire is the stallion »Generale», born 1787, who appears nineteen times in the generations V, VI and VII as follows:

$$\frac{7}{32}+\frac{9}{64}+\frac{3}{128} = \text{genealogical index (see Table 1)} = 38{,}28\ \%.$$

»Troubadour of Willowmore» 6459. Morganbreed in U. S. A.

(Department circular no. 199—1922. United States Department of Agriculture.)

The oldest identified ancestor in his ancestry is the stallion »Justin Morgan», born 1793, who appears 68 times in the generations VIII, IX, X, XI, XII and XIII as follows:

TABLE 1. *Pedigree of the shorthon bull »Comet».*

Young Phoenix								▲ Favourite								Generation I consisting of 2 ancestors, each of 50 % value
● O. Phoenix				▲ Favourite				● O. Phoenix				Bolingbroke				Generation II consisting of 4 ancestors, each of 25 % value
Lady Maynard × ■				● O. Phoenix				Lady Maynard ×				Y. Strawberry				Generation III consisting of 8 ancestors, each of 12,5 % value
				Lady Maynard × ■								Lady Maynard × ◗				Generation IV consisting of 16 ancestors, each of 6,25 % value
																Generation V consisting of 32 ancestors, each of 3,125 % value

Foljambe ■ | Bolingbroke | Foljambe ■ | Foljambe ■ | Foljambe ■ | Y. Strawberry | Foljambe ■ | Dalton Duke ◗ | Dalton Duke ◗

$\frac{13}{256} + \frac{16}{512} + \frac{14}{1024} + \frac{12}{2048} + \frac{12}{4096} + \frac{1}{8192}$ = genealogical index = 10,46 %.

As students of pedigrees will have seen, many individuals belonging to several European breeds exhibit within their four proximate generations of ancestors an inbreeding percentage from 12,5 to 37,5. (Other closer forms will also, of course, often have been observed.) If in its pedigree-table an individual as a minimum of inbreeding, besides the last-mentioned degrees, fails to show any other, older inbreeding, we have reason to believe that the breed in question is not satisfactorily constant. It will often be seen, presumably on account of insufficient inbreeding, that the effect transmitted from a common superior ancestor to the succeeding generations is exhausted and that, within such a breed, the aberrations from a certain definite standard are many and excessively numerous in variety. The fact that the transmitted characters from a common progenitor as years go by seem to have been remodelled is caused, no doubt, by an outcrossing derived from the different female strains. It seems as if the distinct type, referred to, now and then occasionally reappears as a result of inbreeding — called reversion, which is a consequence of Mendelian segregation —, but unfortunately this reappearance occurs sporadically and in different places in the districts of the breed in question. The prepotent influence must therefore be assumed in the main to be lost, because inbreeding in such instances is often carried on unconsciously on account of random matings. In the systematic livestock breeding, even if combined with selection, this method in my opinion will only uphold *status quo* in an unsatisfactory manner, but no real improvement of a breed will result from it.

Through selection from a breed the best specimens at disposal are isolated for the purpose of breeding. Among such individuals only a few, in proportion to the others, distinguish themselves by the capacity of prepotency. But, certainly, in all domestic livestock breeds prepotent individuals occasionally occur. TUFF among other writers in zoötechnical and genetic science maintains that the so-called prepotent males and females are homozygotic in a higher degree than the rest of a breed. Genealogical studies carried on in several countries have shown that in some instances prepotent sires are a result of close inbreeding, whereas in others they are the result of distant inbreeding. Even as a result of more or less remote crossing prepotent sires may appear. Consequently, a homozygotic combination of the inheritable

factors may appear by chance by means of different methods of breeding. PUNNETT'S experiments based upon poultry (gold pencilled Hamburger × Sebright bantams) confirm clearly this view. Close inbreeding, e. g. continued matings of brothers and sisters, is thus no necessary condition for the production of homozygotic individuals.

In livestock breeding the problem of fixation of an inheritable type is, of course, the most important one. It seems to me that SEWALL WRIGHT and TUFF deal insufficiently with one point in this exceedingly important subject. SEWALL WRIGHT maintains that continued matings of brother and sister are a closer form of inbreeding than the connection of half-brothers and sisters, and here he is possibly right. Among other writers WRIGHT and HELEN DEAN KING (1919) have maintained that the former method is the closest possible form of inbreeding in mammals. But is this so? Something must be wrong in the premises upon which this conclusion is based. As will be shown below there is another possible explanation, which ought to be considered. CHARLES DARWIN (1868) in his classic work »Animals and Plants under Domestication» has already discussed whether the mating of brothers and sisters is, or is not, a grosser form of inbreeding than the connection father × daughter, or mother × son. DARWIN himself does not adopt any standpoint as to this question. This was before the Mendelian era! Nowadays, however, there should be no difference of opinion when the discussion is based upon homozygosity as a starting point. Inbreeding, — supposing that this method is used as a means of fixing a definite type in a strain, — can only be carried to its extremity, if a prepotent (homozygotic) individual is mated with son or daughter. The old English constructive breeders, as for instance the brothers COLLING, (see the pedigree of »Comet», table 1) often made use of this form of inbreeding. The reason for the adoption of such a method lies no doubt in the fact that only a few individuals combined in their type all the numerous external characteristics required, and therefore an animal and its offspring had to be mated *inter se* in order to secure a distinguished type. Precisely the same method has to a great extent been utilized by the fixation of the numerous, different types of the pomace-fly, *Drosophila melanogaster*. The first fly which showed any new peculiar character was mated with her offspring. In this way she produced a new strain. This method, the so-called »backcross» [1], is well-known from genetic

[1] The reader will probably be startled by this term, inasmuch as in genetics it means only backcross carried on with a recessive zygote. It matters little to

researches and no better means is known to preserve an occasionally appearing homozygote. This cannot be disputed. In an essay in the Norwegian Veterinary Magazine, December 1921, I have called attention to the very point of the closest possible form of inbreeding. The backcross is just the method which TUFF (1923) has demonstrated on pages 119 and 120, examples I and III. From a genetic systematic point of view I cannot understand that any essential difference exists between the two examples referred to.

In observing several brothers and sisters among our larger kinds of livestock, we have often seen that they vary as regards superiority. As is wellknown, twins are, even among mankind, not always alike, unless they are from the same ovule. In the Congress Edition, (see section II B on page 33) AXEL APPEL (1923) says: »Even brothers are known to have a very different value as sires as regards the yield of their offspring». I have observed the same thing in Norwegian Gudbrandsdal stallions as regards prepotency of certain distinguished external characters. The superior and prepotent stallion Brimin 825 has for instance a brother and also sisters but none of them is equal to him in superiority, some of them being even rather ordinary. In order to preserve his prepotency in the offspring it cannot be the best method to mate him with his own inferior sister. For this purpose one should think it far more rational to mate him with his own superior daughters. As already indicated, among the larger livestock continued matings of brothers and sisters will be exceedingly rare, perhaps with exception of some special cases and only in some few generations within a large stud or herd. Even in these cases among the offspring only a few individuals will be born and some of them will probably not fulfil all requirements from the point of view of a specific, rigid selection. Assuming that dominance is shown in the inheritance of a given character, based upon 5 homomeric factors, we may, according to TUFF, have to expect only one homozygotic individual out of 1024 individuals. This instructive example shows the fact that prepotent individuals seem to be rather a rare phenomenon.

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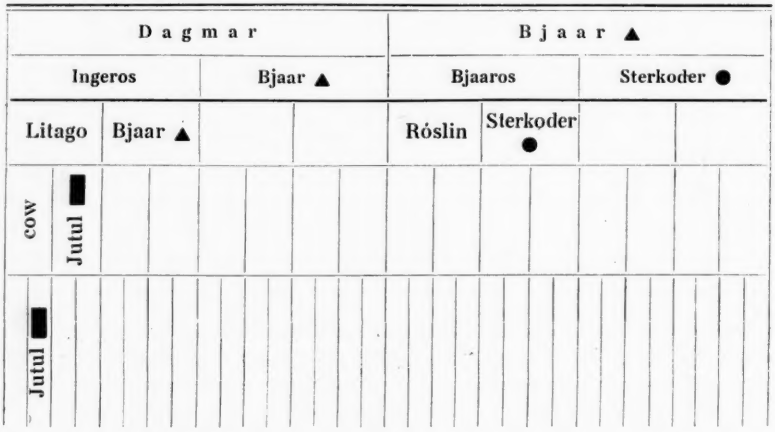
the arguments in this article whether in backcrossing a recessive or a dominant homozygote is employed. Both types of homozygotes, when mated with their offspring, will in the next generation give the highest possible amount of homozygotes, namely 50 per cent *belonging to only one type*, and 50 per cent heterozygotes. The offspring from heterozygotic brother—sister matings in the next generation will, on the other hand, give 50 per cent heterozygotes and 50 per cent homozygotes, but the latter will *belong to two different types*.

In an experiment based upon larger livestock breeds the chance of obtaining a distinguished homozygotic individual is a diminutive one; indeed, even among the results of ever so large a number of matings of brothers and sisters this must be true. When in a breed an individual close up-to-the-definite standard appears, and if this is endowed with the power of transmitting good quality to its offspring, the use of one or more backcrosses should be considered on account of the above-mentioned reasons. Whenever a strain or breed is lacking in constant uniformity it would no doubt be of advantage if the best sires of the leading tribes are obtained through what I would suggest to term »backcross-inbreeding». I am a believer in a »thorough inbred» foundation, provided that it has come from the best sources.

It only remains for me to express my gratitude to Professor TUFF, who in his essay has referred to a method, which I have worked out to give an expression to the degrees of inbreeding. The essay, which Professor TUFF has referred to, was written in December 1920. The said essay was in the form of a reply to PEARL'S methods on the calculations in inbreeding. In the essay I at once mentioned that the studies in the extensive literature on the subject were not yet completed. I have now, however, found that no less an authority than CHARLES DARWIN in his work already referred to has applied, in the main, just the same method in his studies on inbreeding in shorthorns. The case is a very strange one, because none of the writers of text books and papers on livestock breeding, numerous as they are, have called attention to this method at all, as far as I have seen. The percentage of inbreeding gives us the degrees of inbreeding in one numerical expression and is so far a contrast to »removes» and to what the Germans call »freie Generationen». The systems are, in fact, one and the same, but in an other way, in so far as they all are based upon the genealogical index in the lineage ascent of a pedigree — or ancestral table. By use of the genealogical index students of pedigrees will have seen, no doubt, that between matings of brothers and sisters and, on the other hand, backcross mating an essential dissimilarity exists, because the former is based upon two ancestors, but the latter only upon one. It is no doubt an illusion to believe that in livestock between brothers and sisters two individuals should happen to exhibit precisely the same foundation in their complexes of inheritable, ordinary or homomeric factors, which form the basis of the selected qualities, because brothers and sisters vary in their genotypic constitution, as already indicated. Accordingly, in mating brothers and sisters

inter se, production of heterozygotes will be the result, whereas if backcross based upon one, and one only, prepotent (homozygote) individual were used, this would have been avoided. Mating of brother and sister as expressed in the genealogical index shows an inbreeding percentage of 50, based upon two ancestors, whereas the backcross based upon one ancestor gives 75 and, if further carried on, in succeeding generations 87,5 —, 93,75 —, and so on, but a percentage of 100 is of course impossible to reach. The pedigree of the bull »Roland», see TUFF'S essay, pages 120 and 123, shows the high index

TABLE 2. *Pedigree of the Telemark cow »Liljeros».*



of 87,5 % upon the bull »Gubben». In fact, such a pedigree is graded-up by the use of one of the parents. A Telemark cow named »Liljeros», see table 2, has 87,5 upon the bull »Bjaar», but still more surprising is the fact that »Bjaar» himself has an index of 75 upon the bull »Sterkoder», and »Liljeros»'s third dam »Litago» has 75 % inbreeding upon the bull »Jutul». The interesting ancestral table of Comet, see table 1, indicates the following inbreeding percentages, upon: »Favourite» 75 —, »Phoenix» 62,5 —, »Foljambe» 50 —, »Favourite» (cow) alias »Lady Maynard» 40,625 —, »Dalton Duke» 9,375. A comparison between the immediate recent common ancestors in Comet's pedigree and the more remote ancestors in the ascent of Generale Forata, see p. 232, is very interesting; it indicates that inbreeding, even though remote, may lead to a rigid inheritance of a marked type. It deserves notice that a particular quantity of the percentage of in-

breeding, for instance 75 in the offspring, can only be maintained if both the sire and the dam exhibit the same percentage. Now, letting 75 and 50 represent the inbreeding percentage in sire and dam, in the offspring the inbreeding will be 62,5. Thus there seems in all livestock breeding to be a tendency towards outcrossing; inbreeding should therefore now and then be applied in practice in order to prevent want of uniformity.

It is a matter of course, that the quantities here given are only summeric or numerical expressions for the inbreeding in the pedigrees referred to. This method deserves in my opinion attention of students of pedigrees both on account of the easy application and on account of the synopsis which is obtained.

For reasons mentioned above I very much doubt that by SEWALL WRIGHT'S and PEARL'S methods a true estimate of the real homozygosity is procurable. An analysis of the offspring, analogous to that mentioned by Professor TUFF on page 115 in his above mentioned essay, ought to be of paramount importance genetically whether the characteristics in question are based upon homomeric or ordinary factors. With respect to a livestock breed it must be regarded as quite a hopeless task to attempt to produce real homozygotes.

With great truth some writers have characterized inbreeding as a double-edged sword, which should be carefully handled not to wound the person using it. Both inbreeding and a herd-book are important means in the hands of capable breeders, but in the hands of unskilled persons they are of less significance. It should be borne in mind that in all inbreeding the correct estimate both of defects and distinguishing characteristics in the animals mated together depends upon the well-practised eye and on the judgment of the breeder himself. As is well known, in the art of diagnostics neither all physicians nor veterinary surgeons are alike. The true judgment as to whether in a certain case a cure or the lancet should be used depends firstly upon the execution at the right time and in the right place and, secondly, it depends upon no mischance or nothing unforseen occurring. In livestock breeding just the same reasoning will hold true with regard to the problem as to why, or why not, we in a certain case should make use of the closest form of inbreeding.

In modern professional literature, however, this problem, is not so definitely solved as are many problems in medicine. Observations on the moulding of strains and breeds made in practical breeding work ought to be more extensively published and the results compared.

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